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Management of Amphibians, Reptiles, and Small Mammals in North America

Proceedings of the Symposium

July 19-21, 1988
Flagstaff, Arizona



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**July 19-21, 1988
Flagstaff, Arizona**

**Robert C. Szaro, Kieth E. Severson, and David R. Patton
technical coordinators¹**

Sponsored by:

Arizona Chapter of the Wildlife Society

Arizona Game and Fish Department

Northern Arizona University, School of Forestry

USDA Forest Service, Rocky Mountain Forest and Range Experiment Station

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The Management of Amphibians, Reptiles and Small Mammals in North America: Historical Perspective and Objectives¹

Robert C. Szaro²

Historically the management of public lands from a multiple use perspective has led to a system that emphasizes those habitat components or faunal elements that primarily resulted in some sort of definable economic value. While this often benefited other species that were not even considered in the original prescriptions, it also negatively impacted others. We no longer can afford to take this simplistic view of ecosystem management. We need to use a more holistic approach where ecological landscapes are considered as units, and land management practices incorporate all elements into an integrated policy. This includes examining the impacts of proposed land uses on amphibian, reptile, and small mammal populations.

With the passage of the National Forest Management Act of 1976, the monitoring of all renewable natural resources became law. Even with this legislation, most emphasis by National Forests in the United States has been placed on big game, other game species, or threatened and endangered species. Yet, the act lists five

categories of management indicator species: (1) endangered and threatened plants and animals; (2) species with special habitat needs; (3) species commonly hunted, fished, or trapped; (4) nongame species of special interest; and (5) plant and animal species selected because their population changes are believed to indicate the effects of management activities on other species of selected major biological communities or on water quality.

Nongame birds have been the first group to benefit from changing management practices and public concern. The management of nongame birds within the National Forest System received a big boost from the "Symposium on Management of Forest and Range Habitats for Nongame Birds" held in Tucson in May 1975 (Smith 1975). Since that initial symposium, four regional workshops were held emphasizing the management of nongame birds in forest and range habitats (Degraaf 1978a, 1978b; Degraaf and Evans 1979; Degraaf and Tilghman 1980). There have also been Forest Service sponsored symposia targeting specific bird groups such as owls (Nero et al. 1987) and birds using specific habitat features such as snags (Davis et al. 1983).

Only recently has the management of other nongame species gained increased recognition. The landmark symposium on "Herpetological Communities" held in Lawrence, Kansas, August 1977, as part of the

joint meeting of the Herpetologists' League and the Society for the Study of Amphibians and Reptiles, was the first attempt to organize a vehicle for the incorporation of papers dealing with herpetological communities (Scott 1982). Yet, as Gibbons (this volume) clearly shows, little progress has been made in the recognition of amphibians, reptiles, and small mammals as being important focal points for research and management efforts. It is encouraging that recent comprehensive symposia have incorporated papers dealing with these groups. There was an entire session on Amphibians and Reptiles in the symposium "Riparian Ecosystems and Their Management" (Johnson et al. 1985), and almost 30% of the Southern Evaluation Project Workshop reports work on amphibians, reptiles, and small mammals (Pearson et al. 1987).

The intent of this symposium was to bring scientists and managers together to exchange knowledge and ideas on habitat requirements, management needs, and other information on these often overlooked components of North American fauna. Another purpose was to summarize the state-of-the-science of habitats and habitat requirements of species within these groups. Of particular interest were papers emphasizing habitat models, habitat requirements, sampling techniques and problems, community dynamics, and management recommendations.

¹Paper presented at symposium, *Management of Amphibians, Reptiles, and Small Mammals in North America*. (Flagstaff, AZ, July 19-21, 1988).

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The overwhelming response to our announcement for papers was unexpected. More than 60 abstracts were originally submitted for presentation. In order to overcome recent criticism concerning so-called "gray" literature (Bart and Anderson 1981, Capen 1982, Finch et al. 1982, Scott and Ralph 1988), we made every effort to improve the quality of the symposium and its subsequent proceedings. All authors were required to submit their first drafts 5 months prior to the meeting in order to ensure adequate time for peer review and editing. Each manuscript was reviewed by two experts familiar with the topic, and edited for style and content by one of the symposium editors.

We found the meeting itself to be a fertile exchange of ideas and techniques between managers and researchers from all over the country. Those attending found the meeting extremely enlightening both for researchers and managers because of their exposure to new viewpoints. It is a testament to those attending and the quality of the presentations that very little discussion occurred outside the meeting hall when papers were in progress. Virtually all participants were present throughout the symposium, from the first session to the last.

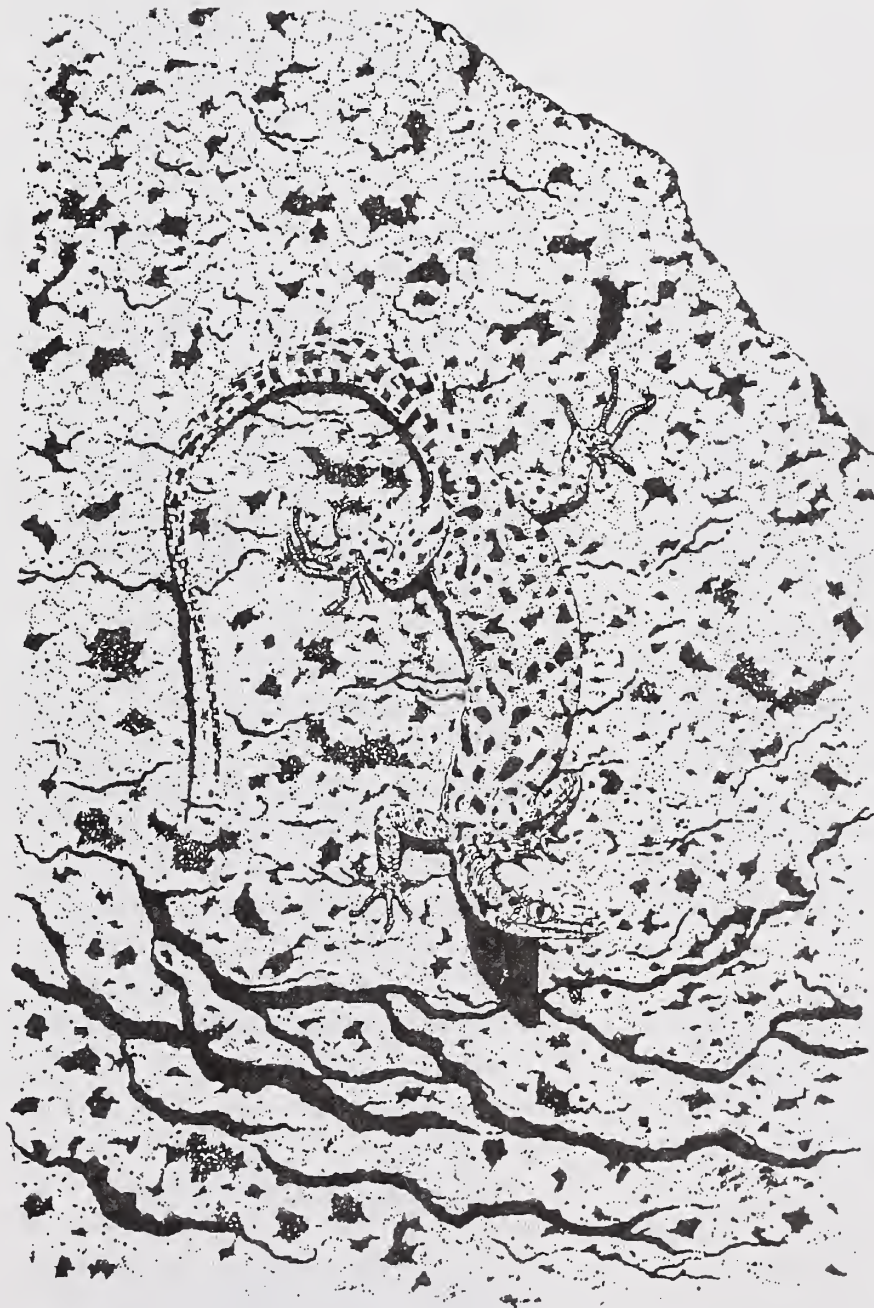
We hope this symposium will prove to be the boost that these faunal groups need to get increased research and management recognition. For only with an adequate data base can models be developed that predict diversity in relation to natural or man-made disturbance of ecosystems. These holistic models are of the utmost importance for the maintenance of worldwide biodiversity (Wilson and Peters 1988). Ecosystem diversity is a key correlate with biological productivity and has recently attracted considerable interest both from theoreticians and from professionals concerned with management of land and water systems (Suffling et al. 1988). We feel that amphibians,

reptiles, and small mammal populations may prove to be the ultimate indicators of habitat quality and health, because of their sedentary characteristics which make them much more susceptible to management activities than do highly mobile bird species and ubiquitous species such as deer and turkey.

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The Management of Amphibians, Reptiles and Small Mammals in North America: The Need for an Environmental Attitude Adjustment¹

J. Whitfield Gibbons²

My objective is to provide an overview and perspective of the amphibians, reptiles, and small mammals of North America as a group that deserves more careful consideration from an environmental management and conservation standpoint. The justification of the need for and timeliness of a careful examination of amphibian, reptile, and small mammal assemblages is based on the premises stated below. One intent is to bring the problem into focus so that both scientists and managers can identify problem areas and conjoin in an effort that will result in the management of these animals in North America in a prudent and far-sighted manner.

I offer four premises to support the contention that amphibians, reptiles, and small mammals deserve special attention with regard to management considerations:

1. Amphibians, reptiles, and small mammals are a significant and important wildlife component of the fauna in most terrestrial and freshwater habitats in North America.

¹Paper presented at symposium, *Management of Amphibians, Reptiles, and Small Mammals in North America*. (Flagstaff, AZ, July 19-21, 1988).

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2. Research and management publication efforts as well as funding have lagged behind those of many of the more obvious faunal components (e.g., game species of large mammals, birds and fishes, and many insects, because of their importance as pests).
3. The direct empirical measurements of habitat requirements, species interactions, and life history patterns needed for proper management are often lacking for amphibians, reptiles, and small mammals.
4. An attitude that amphibians, reptiles, and small mammals should be of concern in environmental management decisions has not been satisfactorily instilled among some managers, the general public, and political officials.

Support for Premises

Premise 1—Amphibians, reptiles, and small mammals are a significant and important wildlife component in North American ecosystems.

One way for a taxonomic group or species assemblage to qualify as im-

Abstract.— Amphibians, reptiles, and small mammals need special consideration in environmental management and conservation because (1) they are significant biotic components in terrestrial and freshwater habitats; (2) research and management efforts have lagged behind those on other vertebrates; (3) a stronger understanding of their ecology and life history is needed to guide management decisions; and (4) their importance has not been promoted satisfactorily to develop the proper public attitude.

portant to an environmental manager is to be identified as making a major contribution to biological complexity in terms of species diversity, trophic dynamics, and interactions within communities. Some groups clearly have the potential for overall community influence by virtue of abundance. Salamanders at Hubbard Brook were demonstrated to have a higher biomass than other vertebrate groups (Burton and Likens 1975). The capture of as many as 88,000 amphibians in one year (SREL Report 1980) and large numbers in most years (Pechmann et al. 1988) at a 1 ha temporary pond in South Carolina suggest that they dominate the higher trophic level in some habitats. Other studies support the postulation that amphibians are often the top predators in some aquatic systems (Taylor et al. in press). Freshwater turtles represent the majority of vertebrate biomass in many aquatic habitats (Congdon, Greene, and Gibbons 1986), and their potential significance as vectors for seeds and parasites among temporary aquatic habitats has been suggested (Congdon and Gibbons 1988). Box turtles (*Terrapene carolina*) have also been implicated as seed vectors (Braun and Brooks 1987). Small rodents are noted for their impact on plant communities under certain environmental conditions (Hayward and Phillipson 1979); desert granivores affect the density, biomass, and composition of annual plants (Brown et

al. 1986). These represent only a few of the available examples for amphibians, reptiles, and small mammals; however, many more studies are needed that document the role and importance of species in these groups in enhancing biological complexity.

Another way for a group to assume importance is for it to have a direct, measurable economic value or impact. Several examples can be given of the importance of amphibians, reptiles, and small mammals from the economic perspective, but their impact has been trivial in comparison to large game mammals or insect pests, and controls and regulations have been comparatively loose. The limited economic importance of most small terrestrial or semi-aquatic vertebrates is presumably one explanation for their being given minimal attention in many management schemes. A few species such as American alligators (Joanen and McNease 1987), bullfrogs (Shiffer 1987), and snapping turtles (Bushey, no date) are commercially important as human food items. Other species assume an economic value in the legal pet trade (Conant 1975) or as research animals sold by biological supply houses (Carolina Biological Supply 1987). Some venomous snakes, especially eastern (*Crotalus adamanteus*) and western (*C. atrox*) diamondback rattlesnakes, are an economic irony in that the venom is necessary to make antivenin (Parrish 1980). Of course, such species achieve some level of importance simply by being potentially injurious. Small mammals have been indicted in a variety of situations for negative economic impacts, such as prairie dog damage (Walker 1983), rabies in bats (Constantine 1970), and grain-eating by rodents (Rowe 1981).

Another measure of importance of some species or groups is the intangible aesthetic value that some people place on them. Many species assume an undeniable importance to many people and may ultimately ac-

Table 1.—Publications on different taxonomic groups in major North American journals in general ecology and wildlife ecology. Issues from 1983-1988 were selected at random until 200 titles were chosen. Assignment to taxonomic categories was based on the appearance of study organism names in the titles. Not all papers used in tabulation were based on North American fauna. The definition of small mammals is that used in this Symposium.

JOURNAL (total)	A	R	S	L	F	B	I
(218) AMN	9	12	43	14	43	18	61
(201) ECOL	10	22	28	10	24	50	58
(213) CJZ	8	9	36	39	34	53	34
(614) Total	27	42	107	63	101	121	153
%	4	7	17	10	16	20	25
(139) HSI*	1	4	4	13	50	67	—
(204) JWM	0	2	6	103	—	93	—
(343) Total	1	6	110	126	50	160	—
%	<1	2	3	37	15	47	—

General Ecology	
A = Amphibians	AMN = American Midland Naturalist
R = Reptiles	ECOL = Ecology
S = Small mammals	CJZ = Canadian Journal of Zoology
Wildlife Ecology	
F = Fishes	HSI = U.S. Fish and Wildlife Service Habitat Suitability Index Models
B = Birds	JWM = Journal of Wildlife Management
I = Insects	

*Only 139 titles were available.

quire protected status. Legal protection of "the species" often provides protection to certain habitats. This circle of protection is a factor that can work to great advantage for those persons interested in preservation—the species is protected because it is important (aesthetic) and becomes even more important (legal) because it is protected and results in preservation of the habitat. For example, the legal status offered the desert tortoise (*Xerobates agassizi*; Luckenbach 1982) and the Morro Bay kangaroo rat (*Dipodomys heermanni morroensis*; USDI 1980) in California or the American crocodile (*Crocodylus acutus*; Kushlan and Mazzotti 1986) in Florida serves to provide some level of environmental protection for the entire community where they occur. The protection given the black footed ferret has resulted in protection of its prey. The World Wildlife

Fund recognizes this effect in its conservation programs by designating "flagship" species such as great apes or monkeys, for which funds are more easily raised, in order to protect entire communities or ecosystems.

Premise 2—Ecological research on herpetofauna and small mammals has lagged behind that of other animal groups.

Support for the contention that the level of ecological research on amphibians, reptiles, and small mammals is lower than that of certain other animal groups can be given in several ways. These include annual publications on particular groups (table 1) and the proportion of funded grants that fall into each category (table 2).

The reasons for the lower levels of publication and funding in research on amphibians, reptiles, and small mammals are varied and in part conjectural. One seemingly obvious reason is that most species in these groups have low profile in health, hunting, agricultural, or other economic issues and therefore receive minimal attention from some quarters. The comparatively low level of attention given to small, non-game terrestrial and semi-aquatic vertebrates by certain sectors of society is reflected in lower overall funding and subsequently in fewer general publications.

Research funding is inequitable because of the emphasis on species that have important economic status; thus, the life history and ecology of even moderately abundant herpetofaunal or small mammal species are seldom understood at a level that would permit prudent management. Even those with potential economic importance receive less emphasis than many birds, large mammals, and fish. As an example, the American alligator represents a reptile species of vital concern from a manage-

ment standpoint, yet the number of publications that focus on the life history, ecology, behavior, and genetics of the species is limited (see Brisbin et al. 1985) compared to the hundreds on large mammal game species such as white-tailed deer (Halls 1984; Johns and Smith 1985).

Premise 3—The basic ecological and life history information necessary to make thoughtful environmental management decisions is often absent for many of the amphibians, reptiles, and small mammals in a community.

As indicated above, the research effort directed toward amphibians, reptiles, and small mammals by ecologists appears to be below that for other vertebrate groups. Although difficult to measure, it would also be expected that the fundamental data bases necessary for thoughtful management decisions would exist in lower proportions for herpetofaunal and small mammal species. One reason is that, compared to many large mammals, birds, and

fishes, certain aspects of field studies on many of the amphibians, reptiles, and small mammals are sometimes perceived as being more difficult because of factors such as small body or population sizes, fossorial or cryptic habits, patchy distribution, and unpredictable seasonality. Consequently, fewer papers are likely to be published in general ecology journals that expect quantitative ecological and life history research results rather than ones that are descriptive and qualitative. An exception to this may be manipulative field experiments in which small rodents have been used in almost half of the studies involving vertebrates.

The actual or apparent rarity or unpredictability of occurrence of many amphibian, reptile, and small mammal species makes it difficult or impossible for the research ecologist to gather useful data without a funding base that is accepting of the uncertainty of whether data will actually be forthcoming in a particular year. The environmental manager in turn cannot incorporate such species into a management plan, and thus their perceived importance is diminished. The unpredictability of occurrence of some species can be demonstrated with amphibians and reptiles on the Savannah River Plant (SRP) in South Carolina. In spite of more than a quarter of a century of field studies and the capture of more than half a million reptiles and amphibians across all available habitats, species previously unreported from the SRP continue to be discovered (Gibbons and Semlitsch 1988; Young 1988). Or, some species have gone for intervals as long as one decade (e.g., pickerel frog, *Rana palustris*) or two (e.g., glossy water snake, *Regina rigida*) between sightings (Gibbons and Semlitsch 1988). Clearly, developing a basic ecological field study on such species in a region is not feasible under typical funding situations.

Resolutions to the problem of garnering information about rare species include intensifying survey efforts in

Table 2.—Number of grant proposals funded by selected U.S. granting agencies on particular groups of animals.

	A	R	S	L	F	B	I
NSF (1987)	1	3	4	2	11	7	24
Sigma Xi (March 1987)	4	8	9	7	9	24	10
National Geographic (1988)	0	3	2	28	8	15	14
World Wildlife Fund (1987-1988)	0	15	0	49	0	14	1
Total	5	29	15	86	28	60	49
% 2	11	6	32	10	22	18	

A=Amphibians
R=Reptiles
S=Small mammals
L=Large mammals
F=Fishes
B=Birds
I=Insects

geographic regions of interest by supporting long-term research programs that can ultimately reveal the presence of rare or fossorial species. Once a species is identified to be present in a habitat, the decision should be made on whether an ecological research effort is warranted.

Long-term studies may be necessary to reveal certain life history traits, even about common species, because of the inherent variability in some life history features that can result from natural environmental variation (Semlitsch et al. 1988). Such studies may be essential to identify the extent of variability due to annual weather patterns and climatic variation (Semlitsch 1985; Pechmann et al. 1988). Long-term research programs may be needed because some species are long-lived, or in the case of many, because the potential longevity is great but unknown (Gibbons 1987).

For many species that have economic value (e.g., snapping turtle, *Chelydra serpentina*; Congdon et al. 1987), the impact of harvesting has not been properly assessed. Because of the limited baseline ecological and life history data for most species, a priority goal should be the establishment of a moratorium on the wholesale removal of all native species of amphibians, reptiles, and small mammals until it can be verified that regional populations can sustain the removal rate. State permits should be required of, and possession limits should be set for, all commercial collectors for all species of amphibians, reptiles, and small mammals.

Today's emphasis should be on protection of each species until convincing evidence is supplied that harvesting has no long-term impact, rather than placing the burden on herpetologists and mammalogists to demonstrate population irrecoverability before harvesting is discontinued. The negative consequences of the latter, and current, approach (i.e., demonstrating the impact of removal while harvesting is in progress) is

that some populations will be reduced to the point of no recovery before the necessary evidence can be collected. Each species should be protected until proven harvestable. The appropriate basic research should be conducted by scientists with no economic or emotional investment in the outcome. Research support should be provided by state or federal agencies and by special interest groups that have no influence over the final management decisions. The ideal approach is that scientists would gather the facts and that environmental managers would interpret them in the context of harvesting quotas. The development and use of predation (Holling 1966) or harvest (Ricker 1975) models may be effective approaches for addressing the issue of human predation (i.e., harvestability by man).

One area that deserves attention in strengthening the study of small terrestrial or semi-aquatic vertebrates is the use of innovative techniques to address physiological, ecological, and behavioral questions under natural conditions. Non-destructive field sampling techniques are critical in the study of both rare and endangered species but are also important for preserving the integrity of any study population. These include techniques for capture, field identification of individuals, non-disruptive handling or observation, recapture, and the acquisition of non-destructive physiological, genetic, behavioral, and life history data. Some examples include radiography (Gibbons and Greene 1978) or sonography for determination of clutch sizes, blood sampling for genetic and hormonal analyses (Scribner et al. 1986), and cyclopropane for measuring lipid levels (Peterson 1988). A broader use of such techniques in field studies could strengthen the foundation of ecological and life history understanding that is necessary for environmental management.

A direct contribution to environmental managers could be achieved

by attempts to verify the several amphibian, reptile, and small mammal Habitat Suitability Index models of the U.S. Fish and Wildlife Department. The concept has the potential value of providing an initial quantitative approach that gives a tangible product. However, to be of greatest value, the HSI models must be evaluated and modified as appropriate. It is perhaps noteworthy that the HSI models prepared for amphibians (1), reptiles (4), and small mammals (4) collectively represent only 6% of the 139 that have been completed on vertebrates (table 1). For these to become an effective tool in management of herpetofauna and small mammals, more herpetologists and mammalogists need to volunteer to develop HSI models for these groups.

A distinction must be made between (1) problem oriented applied research on specific systems that relies on qualitative assessments or indirect measurements of variables with minimal inference power and (2) basic research that is founded on quantitative or direct measurements of variables, has a conceptual or theoretical base or orientation, and can be strongly inferential through general field or laboratory experiments. The latter approach will be necessary if environmental managers are to have a reliable data base that is founded on broad applicability, levels of predictability, and clear directions for future research.

Premise 4—The attitude of most people in North America toward most amphibians, reptiles, and small mammals is either negative or neutral, in part because efforts to develop an attitude change have been insufficient or ineffective.

Although documentation is difficult, it would appear that in North America we are far from a suitable acceptance level toward these groups of

organisms. People still try to run over snakes on highways, have little awareness that many conspicuous predators rely on small mammals for their basic diets, and give no thought to how many small vertebrates will be eliminated by the draining of a swamp or damming of a stream. I think the situation is an embarrassing one for the scientists and general public of a nation that espouses education and knowledge.

Evidence that a more positive attitude and less environmental leniency has developed over the last several years is the recent federal listings of snakes (e.g., indigo snake, *Drymarchon corias*; San Francisco garter snake, *Thamnophis sirtalis tetrataenia*) and small rodents (e.g., Utah prairie dog, *Cynomys parvidens*; salt marsh harvest mouse, *Reithrodontomys raviventris*; Key Largo cotton mouse, *Peromyscus gossypinus allapaticola*) as protected species. However, many of the listings involving amphibians, reptiles, and small mammals have been hard fought ones against public and political opinions that such species hardly deserve such concessions. The failed efforts at protection far outnumber the successful ones. The attitude that these animals are unimportant is pervasive throughout the general public, politicians, and even some environmental managers. The basic responsibility for eliminating ignorance and effecting the proper environmental attitude adjustment must start with the scientist.

It is my firm opinion that many scientists have lost sight of who their patrons are (for most of us, the U.S. taxpayers) and of their responsibility to communicate findings to all levels of society. This communication process entails a level of cooperation and an educational spirit that allows each individual to contribute in the most effective manner. However, we must all accept and work toward the common goals of establishing a thorough and general foundation of ecological information for amphibians, reptiles, and small mammals and of being

generous in the distribution of the findings in a form palatable to and usable by the intended audience.

Conclusions

An environmental attitude adjustment model must be developed and promoted that considers where we want to end up, who we must educate and influence, and what we must know and do to achieve the goal of education in a convincing manner. The desired end point is a nationwide attitude among scientists, managers, politicians, and the public that amphibians, reptiles, and small mammals are critical wildlife components. Each species population and community must be identified as having an intrinsic value in maintaining the integrity of the natural ecosystems of North America.

Scientists have a responsibility for collecting extensive and intensive information on the life history patterns and habitat requirements of native amphibians, reptiles, and small mammals. The required data must be collected in a rigorous experimental manner that promotes an understanding of these species and communities through strong inferences and syntheses.

Politicians have a responsibility to assure that the approval of a government project is as contingent on environmental consequences as on budgetary considerations. Our attitude must graduate to become one of acceptance of a proposed project only after environmental impact determinations have led to an objective decision that the gain from the project warrants the loss to the environment.

Managers have a responsibility for promoting basic research, for applying the findings to habitat management, and for having the patience to wait for the completion of long-term studies as required. In situations where removal of animals or elimination of habitat is an issue, the burden of proof should be borne by the har-

vester or developer, and not by the scientist or manager. The status of a species should be determined before the decision to proceed is made, certainly not after harvesting begins or during the physical development of a project. This assessment should be made and evaluated before the project is approved. Each species should be protected until proven harvestable.

Both scientists and managers have a responsibility to inform the public and political arena that the protection and ecological understanding of inconspicuous and non-game species are vital to proper ecosystem management and to the preservation and maintenance of North America's natural heritage.

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Douglas-fir Forests in the Oregon and Washington Cascades: Relation of the Herpetofauna to Stand Age and Moisture¹

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The value of old-growth forests for wildlife is highly debated (Fosburg 1986, Harmon et al. 1986, Harris 1984, Kerrick et al. 1984, Ruggiero and Carey 1984, Salwasser 1987, Wilcove 1987). Most attention has been directed toward the spotted owl (*Strix occidentalis*), which is one of several hundred vertebrate species occurring in the Pacific Northwest (Bruce et al. 1985). Franklin and Spies (1984) distinguished old-growth forests of Douglas-fir (*Pseudotsuga menziesii*) as having a wide range of tree sizes and ages, a deep multilayered crown canopy, large individual trees, and accumulations of coarse woody debris (CWD), including snags and downed logs of large dimension. They reported that these forests are productive, diverse ecosystems, and highly specialized habitats.

We need to evaluate sampling techniques continually to better describe, understand and predict the species richness, abundance and biomass of herpetological assemblages. However, few herpetological communities or their habitats have been

sampled using more than one quantitative technique.

Recently, field techniques for the study of herpetological communities have improved (Scott 1982). Some of the most promising methods employ pitfall traps and drift fences to capture amphibians and reptiles. Several promising pitfall designs have been developed for varied habitats in Australia (Friend 1984, Webb 1985) and in North America (Bennett et al. 1980, Bury and Corn 1987, Bury and Raphael 1983, Campbell and Christman 1982, Enge and Marion 1986, Gibbons and Semlitsch 1981, Jones 1981, 1986, Raphael 1984, Raphael and Rosenberg 1983, Rosenberg and Raphael 1986, Vogt and Hine 1982). Pitfall traps are effective for capture of common terrestrial species and they are particularly valuable in sampling secretive or rare forms.

Searches by hand (either based on specific areas or time of collecting) or observation are used to sample herpetofaunas (see reviews by Bury and Raphael 1983, Jones 1986, Pough et al. 1987). Campbell and Christman (1982) suggested that time-constrained collecting (searching within a specific period of time by trained collectors) can sample terrestrial species that are under-sampled or not taken in pitfall traps.

The first year of our old-growth study (1983) was partly devoted to refining field techniques. A comparison of different pitfall designs is reported elsewhere (Bury and Corn

Abstract.—Pitfall traps effectively sampled amphibians but not reptiles in Douglas-fir (*Pseudotsuga menziesii*) forests. The abundance of only one amphibian species varied across an age gradient or a moisture gradient. Salamanders and frogs that breed in ponds or streams were captured in large numbers in some stands, likely due to the presence of nearby breeding habitat rather than forest conditions. Lizards occurred mostly in dry stands and clearcuts. Time-constrained searches showed different use of downed woody debris among terrestrial salamanders. The occurrence and abundance of species in naturally regenerated forests markedly differed from clearcut stands.

1987). Here, we employ a standardized pitfall array and time-constrained searches to determine the occurrence and abundance of the terrestrial (upland) herpetofauna in the Cascade Mountains of the Pacific Northwest.

The current work on small mammals (Anthony et al. 1987, Corn et al. 1988, West 1985), birds (Carey 1988, Manuwal and Huff 1987), and bats (Thomas *in press*) are part of an interdisciplinary effort to better understand the relationship of nongame wildlife in old-growth forest stands (Ruggiero and Carey 1984). Our study is the first to attempt to identify which species of the herpetofauna, if any, are associated with age and moisture gradients in forests of the Cascade Mountains.

Our specific objectives were (1) to compare effectiveness and relative merits of time-constrained collecting versus pitfall trapping, (2) to compare the species richness and relative abundance of amphibians and reptiles between different forest stands, and (3) to examine the association of the herpetofauna with old-growth forest conditions.

DESCRIPTION AND CLASSIFICATION OF STUDY SITES

We sampled 30 sites: 18 in or near the H. J. Andrews Experimental Forest in eastern Linn and Lane counties, Oregon, and 12 stands in the

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Wind River Experimental Forest, Skamania County, Washington. All sites are on the western slopes of the Cascade Mountains. Specific locations, stand classification, elevations and other details are provided in Corn et al. (this volume).

Study sites represent a range of forest development across a chronosequence (principally age) and, for old-growth, a moisture gradient. These stands were independently selected and assessed by Spies et al. (*in press*). They were all in naturally regenerated forest caused by wildfire. There were three development stages in moderate moisture conditions: young (30-76 years old), mature (105-150 years) and old-growth (195-450 years). Clearcut sites represent recent timber harvest (<10 years old). For old-growth stands only, there were representative moisture conditions: wet, moderate and dry sites. Stand classification was based on age determined by increment boring of trees or other methods, characteristic plant species in the understory, physiography, and soils. These methods and other parameters are described by Corn et al. (this volume), Franklin et al. (1981) and Spies et al. (*in press*).

Following the initial stand selection, there were minor adjustments in assignment of stand classification (Corn et al., this volume). We rejected a few sites that were either not continually accessible for our weekly checking of pitfall traps or were being actively logged.

MATERIAL AND METHODS

Time-Constrained Searches (TCS)

Details of this technique are provided elsewhere (Campbell and Christman 1982, Bury and Raphael 1983, Raphael and Rosenberg 1983). A team of 3-8 people intensively searched each stand for 8 person-hrs in the spring (8-25 April 1983 in Oregon and 3-12 May 1983 in Washing-



Figure 1.—Conducting time-constrained searches in an old-growth stand, Oregon. Note large amounts of downed woody debris.

ton). We turned over moveable surface objects (twigs to logs <1 m diameter), dug into decayed wood, and removed bark from downed wood or the bases of standing snags by hand or with potato rakes (fig. 1).

Collectors remained within boundaries of habitat typical of the stand, avoiding conspicuous specialized habitats such as ponds, creeks or rock outcrops. Further, we searched 4 sites in each state again during warm weather (July-Aug 1983). These surveys were performed for 4 hrs per plot. We recorded information on exact position of capture for each animal, including vertical position (e.g., on or under litter; on, under or in log; etc.), identification of cover object, length and diameter of object, time of capture, total length, and mass of animal.

We determined the decay class of coarse woody debris occupied by animals on the forest floor. Large woody debris or felled trees (logs) occur in five progressive broad decay classes (Bartels et al. 1985, Franklin et al. 1981, Harmon et al. 1986, Maser et al. 1979, Maser and Trappe 1984): (1)

intact, recently downed trees; (2) logs with loose bark; (3) loss of bark and stem partly rotted; (4) invasion of roots and deep decomposition of stem; and (5) hummocks of wood chunks and organic material. Once fallen, a large tree might require 200 or more years to progress from class 1 to 5 (Spies et al. *in press*), providing habitat for many generations of resident wildlife.

Pitfall Arrays

We installed a pitfall array at each site in Oregon and Washington (details in Bury and Corn 1987). Each array had two triads with their centers 25 m apart. Each triad was composed of three drift fences 5 m long and 0.5 m tall; about 0.3 m of fence was above ground. Fences radiated at 120° angles, beginning 3 m from the center point. The compass directions of the arms depended on openings between trees or large logs on the forest floor. Pitfall traps were constructed from two stacked #10 tin cans (3.2 l volume) connected with

Table 1.—Numbers of amphibians and reptiles captured during time-constrained searches (TCS) conducted 8-25 April 1983 at the H. J. Andrews Experimental Forest in Oregon. Old-growth stands are arranged in order of increasing dryness.

Species	Stand No.	Old growth																	
		Wet			Moderate			Dry			Mature			Young			Clearcut		
		15	03	24	02	17	33	25	29	11	35	42	39	47	48	75	55	291	391
Clouded Salamander			3	8	6	9		3	11	17	4		2			1	2	12	2
Oregon Slender Salamander	2	6	4	12	9					11	5	1			9	1		1	
Oregon Ensatina	4	3	1	9	5	7	22	2	10	6	4	5	3	9	8	9	4	1	
Dunn's Salamander					2			1											
Rough-skinned Newt					2												1	1	
Pacific Tree Frog									1		4		1					1	1
Western Skink																	1		
Northern Alligator Lizard																	1		
Western Fence Lizard																	2		

^aTwo surveys were conducted in this stand and the results are combined here.

duct tape. A pit trap was placed flush with the ground surface at each end of the fence. Funnel traps were constructed of aluminum screening, rolled into a tube 1 m long by 0.1 m diameter, with inward funnels stapled at each end of the trap. A funnel trap was placed midway on either side of the fence. No water or preservatives were added to the traps. A wooden shingle was propped over each pitfall and funnel trap, but water entered pit-

falls during heavy rains. We routinely removed water from traps with scoops or a hand-operated aquarium siphon.

We operated pitfall traps continuously for 180 days, from the last week of May to late November 1983. Traps were checked 1-2 times each week. Captures were usually taken to a field laboratory for identification and measurements. All retained specimens are deposited at the National Museum of Natural History.

RESULTS

Time-Constrained Searches (TCS)

Yield

During spring TCS, we collected 258 amphibians and 4 reptiles (table 1) at the 18 Oregon sites (1.8 animals per person-hr) and we took 78 amphibians and 4 reptiles (table 2) at 12 Washington sites (0.85 per person-hr). For summer TCS, all Washington captures included only 4 lizards from one clearcut, one mature (drier aspect) and an old-growth dry stand (0.25 animals per hr) whereas in Oregon we captured 13 salamanders (no new species) and 2 lizards from 4 sites (0.9 animals per hr).

Although we report the abundance of herpetofauna collected by TCS (tables 1 and 2), we did not analyze these results based on the age and moisture gradients because such abundance data can be biased.

Habitat Use

TCS provided useful information on the exact position where individuals were found (table 3). Oregon ensati-

Table 2.—Numbers of amphibians and reptiles captured during TCS 3-12 May at the Wind River Experimental Forest in Washington. Old-growth stands are arranged in order of increasing dryness.

Species	Stand No.	Old growth											
		Wet			Moderate			Dry			Mature		
		14	12	21	20	31	41	42	50	60	61	70	71
Olympic Salamander	2												
Oregon Ensatina	3	7	13	5	5	4	1	1	1	1			
Larch Mountain Salamander		14											
Western Red-backed Salamander			6										
Rough-skinned Newt				3	2					1			
Red-legged Frog	1												
Pacific Tree Frog												1	
Rubber Boa								2				1	
Common Garter Snake						1							

Table 3.—Number of salamanders (Oregon data only) captured in different microhabitats. Percentages are in parentheses.

Position	Oregon Ensatina	Clouded Salamander	Oregon Slender Salamander
On/Under Litter	3 (2.4)	0 (0)	1 (1.6)
On/Under Rock	3 (2.4)	0 (0)	1 (1.6)
On/Under Log	14 (11.5)	8 (10.2)	6 (6.8)
Inside Log	52 (42.6)	27 (34.2)	38 (62.3)
Under Bark on Log	12 (9.8)	37 (46.8)	7 (11.5)
Under Bark on Ground	38 (31.1)	7 (8.9)	8 (13.1)

nas (*Ensatina eschscholtzi*; fig. 2) occurred more evenly and in more microhabitats than did the other two species. Clouded salamanders (*Aneides ferreus*) were mostly under bark on logs and, secondarily, often were in logs (81% of the sites occupied were related to logs). The Oregon slender salamander (*Batrachoseps wrighti*) predominately occurred in logs (62%) and then under bark on ground or on logs (87% in or near logs). Most bark on the ground occurred in piles sloughed from fallen trees or snags and is essentially an extension of the log environment.

Terrestrial salamanders that were captured in or near downed wood markedly differed in their use of different decay classes of CWD (fig. 3).

We did not include decay class 1 logs, because few of these were searched and none had salamanders. These logs are intact material and offer little cover for salamanders.

We calculated Chi-square statistics for three species in Oregon. The clouded salamander was most abundant in younger (class 2) logs ($P < 0.001$), while Oregon slender salamanders were found more often than expected in the more decayed class 4 and 5 logs ($P < 0.05$). Numbers of Oregon ensatina generally followed the pattern of log abundance (fig. 3), except that they were found less often than expected in class 3 logs ($P < 0.05$). These results are consistent with microhabitats where the salamanders were captured (table 3).



Figure 2.—Adult ensatina (*Ensatina eschscholtzi*) from Douglas Co., Oregon.

Pitfall Trapping

Total Numbers

Pitfall arrays at 18 Oregon sites provided 1,028 captures (table 4): 685 salamanders, 252 frogs, 64 lizards and 27 snakes. Pitfalls at 12 Washington sites yielded 1,152 animals (table 5): 460 salamanders, 663 frogs and 29 snakes. Two Washington sites had exceptional catches: 253 tailed frogs (*Ascaphus truei*) at #21 Old-growth Moderate and 119 red-legged frogs (*Rana aurora*) at #42 Mature.

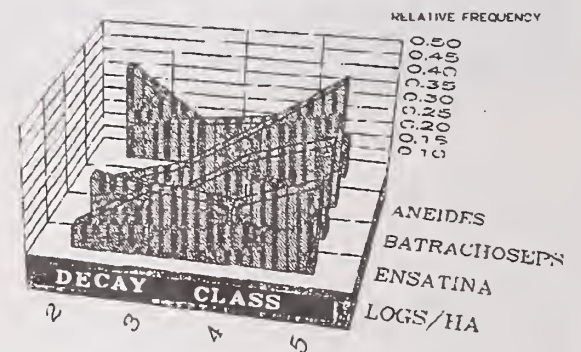


Figure 3.—Frequency of occurrence of clouded salamanders, Oregon slender salamanders, and Oregon ensatinas occupying downed wood in decay classes 2-5. Density of logs in each decay class are provided. Data are from 18 sites at the H. J. Andrews Experimental Forest, Oregon.

Yield

Summer operation of the pitfall arrays added a few reptiles but the bulk of the catch was amphibians in the fall months during and after heavy seasonal rains (Bury and Corn 1987). There was a low catch of reptiles (Oregon, mean = 5 per site; Washington, mean = 2.4).

Species richness did not differ across the chronosequence gradient (table 6, fig. 4). Moderate and dry old-growth stands had the highest mean abundance across the moisture gradient, which was caused by the capture of large numbers of several migratory species.

Table 4.—Abundance of amphibians and reptiles captured by pitfall arrays at the H. J. Andrews Experimental Forest in Oregon. Arrays of pitfall traps with drift fences were operated continuously for 180 days in 1983. Old-growth stands are arranged in order of increasing dryness.

Species	Stand No.	Old growth									Mature			Young			Clearcut		
		Wet			Moderate			Dry											
		15	03	24	02	17	33	25	29	11	35	42	39	47	48	75	55	291	391
Northwestern Salamander								1	27			5		1		1		8	1
Pacific Giant Salamander					1				7				2			2	1	1	
Clouded Salamander			1	2	1			2	4				1	1				3	1
Oregon Slender Salamander	1	3	1			1					1			4			1	1	
Oregon Ensatina	8	2	10	18	22	13	26	21	9	15	10	16	14	20	30	12	10		1
Dunn's Salamander							1	1											
Rough-skinned Newt	21			3	26	5		119	62			15		13	36	5	14	16	2
Tailed Frog			28	5	3	4	17		46	7		6	28		30			3	
Red-legged Frog									23		28					2		4	
Pacific Tree Frog	2										3		1		3	3		2	5
Western Skink									3								11	9	
Norhtern Alligator Lizard						1		3	4								14	8	2
Western Fence Lizard								1									5	3	
Rubber Boa															1				
Northwestern Garter Snake	1				2	1											1	11	
Common Garter Snake	1	1	2				1					1		2	1			1	

Table 5.—Abundance of amphibians and reptiles captured by pitfall arrays at the Wind River Experimental Forest in Washington. Arrays of pitfall traps with drift fences were operated continuously for 180 days in 1983. Old-growth stands are arranged in order of increasing dryness.

Species	Stand No.	Old growth												
		Wet			Moderate		Dry	Mature			Young		Clearcut	
		14	12	21	20	31	41	42	50	60	61	70	71	
Northwestern Salamander			2	5	15	4	1	1	1	9	10	2		
Pacific Giant Salamander				1										
Olympic Salamander	3			1			1							
Oregon Ensatina	7	35	29	18	39	14	13	3	24	25	0	1		
Larch Mountain Salamander			10											
Western Red-backed Salamander			19											
Rough-skinned Newt	10	4	5	40	1	10	4	7	38	37	7	4		
Tailed Frog	44	22	253	4	27	50	4		2	1	4			
Red-legged Frog	8	1	3	15		1	19	119	40	5	23	6		
Pacific Tree Frog								3				9		
Northern Alligator Lizard					1			1		12	1			
Northwestern Garter Snake					2	1				4				
Common Garter Snake			6										1	

Differences in Closed-Canopy Stands

For Oregon and Washington data combined, mean abundance of common species (3 salamanders, 2 frogs) appeared to differ across either forest development (age) or moisture gradient (fig. 5). However, except for the Oregon ensatina, none of the differences were statistically significant (table 6). High numbers of individuals at a few stands resulted in large variances in catch at stand types.

Large numbers of both the rough-skinned newt (*Taricha granulosa*) and Northwestern salamander (*Ambystoma gracile*) were captured in a few stands (tables 4-5). Most of the tailed frogs taken were juveniles at one old-growth site in Washington (table 5), and these were apparently dispersing away from a nearby stream. Similarly, most (78%) of the red-legged frogs were taken at 5 sites (tables 4-5); the largest number ($n =$

119) were juveniles captured at one mature stand in Washington.

The only species showing a significant difference (table 6) across the chronosequence of stands was the Oregon ensatina. Its numbers were lower in mature stands (fig. 5), perhaps related to amounts of CWD in different age classes (fig. 6). Abundance of Oregon ensatinas was most highly correlated with the number of decay class 4 and 5 logs per hectare (Pearson $r = 0.48$, $n = 29$, $P < 0.01$) and the mean diameter (d.b.h.) of large-sized canopy trees ($r = 0.51$, $n = 29$, $P < 0.01$). A discussion of the habitat variables used here is provided in Corn et al. (1988). Mean abundance of Oregon ensatina also differed across the moisture gradient in old-growth stands with fewer present in wetter sites than drier. Paradoxically, most OGW stands have large amounts of CWD (fig. 6). Oregon ensatina may be associated with the amount of CWD, but there are other components of the habitat that may be underrepresented in OGW stands.

Clearcut Stands

We also trapped 5 clearcut sites (all <10 years old) to describe herpetofauna occurrence in managed

stands. The relative abundance of the herpetofauna in these clearcuts markedly differed from 6 comparable young stands (fig. 7). Reptiles predominate in clearcuts, most likely responding to increased ambient temperature in such areas. The Pacific treefrog (*Hyla regilla*) also was most abundant in clearcuts.

DISCUSSION

Comparison and Improvements in Techniques

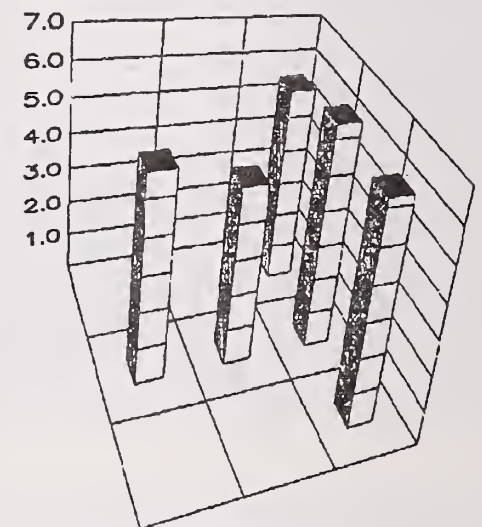
Time-constrained searches (TCS) provided insufficient animals for quantitative analyses in most stands. The technique might be more worthwhile under optimal environmental conditions (e.g., after heavy rains for amphibians) and with increased effort (16+ person-hr per site). Summer searches added the occurrence of lizards to some stands, but in general the effort was not worth the time investment in forested stands of the Cascade Mountains.

However, TCS can be effective to sample terrestrial species of salamanders. Our pitfall trapping (180 days) caught 257 ensatina, 44 clouded salamanders, and 13 Oregon slender salamanders, whereas TCS yielded 113 ensatina (0.44 times that of pit-

falls), 76 clouded salamanders (1.7 X pitfalls), and 57 slender salamanders (4.4 X pitfalls). The clouded salamander is a common denizen of Oregon forests and sometimes the most frequently encountered species, but pitfall traps caught few. This species has large toes and is adept at climbing, and perhaps escaped. Or, they rarely free-fall into traps on the ground. The Oregon slender salamander seems to be associated with

SPECIES RICHNESS

MEAN # OF SPECIES



ABUNDANCE

MEAN TOTAL CAPTURES

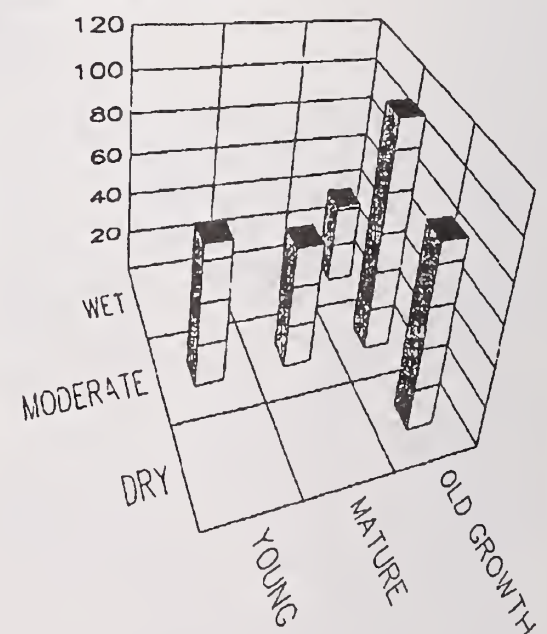
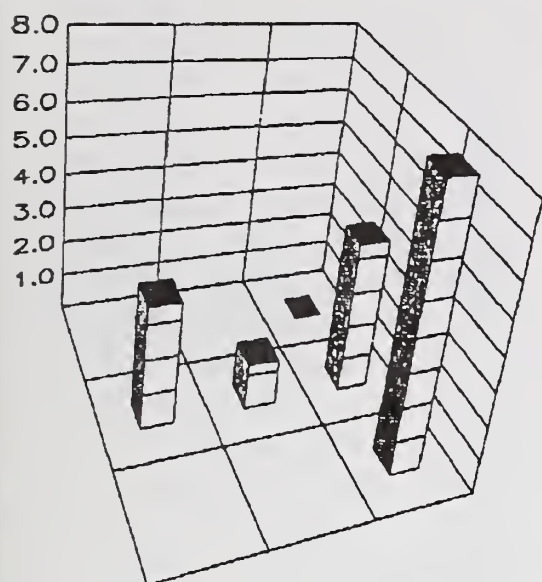


Figure 4.—Mean species richness and mean total abundance of amphibians and reptiles in closed-canopy forest stands.

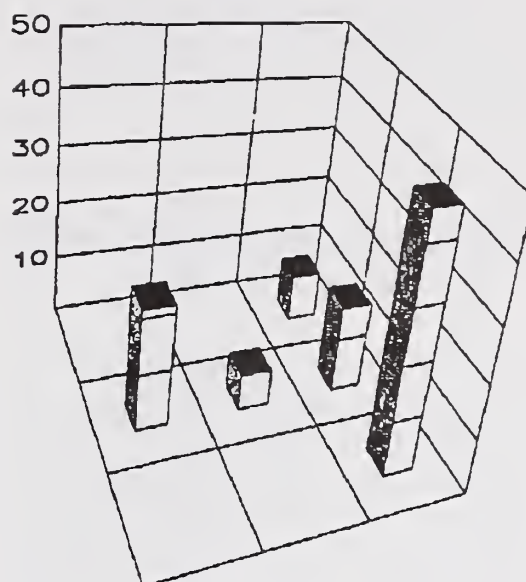
Table 6.—Analysis of variance of species richness and abundance (log transformed) categorized by age (old growth, mature, and young) and moisture (wet, moderate, and dry). Wet and dry old growth stands were not used in the analysis of stand age, and mature and young stands were not used in the analysis of stand moisture.

	Age (n = 17)		Moisture (n = 13)	
	F	P	F	P
Species Richness	2.02	0.17	0.30	0.75
Total Abundance	0.92	0.42	2.40	0.14
Northwest Salamander	0.38	0.69	1.90	0.20
Rough-skinned Newt	0.91	0.43	0.26	0.78
Oregon Ensatina	8.09	0.005	11.4	0.003
Tailed Frog	0.92	0.42	0.06	0.94
Red-legged Frog	0.65	0.54	0.12	0.89

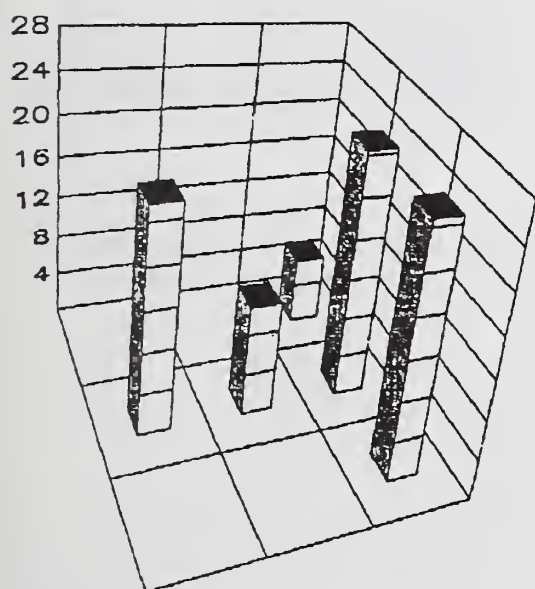
Ambystoma gracile



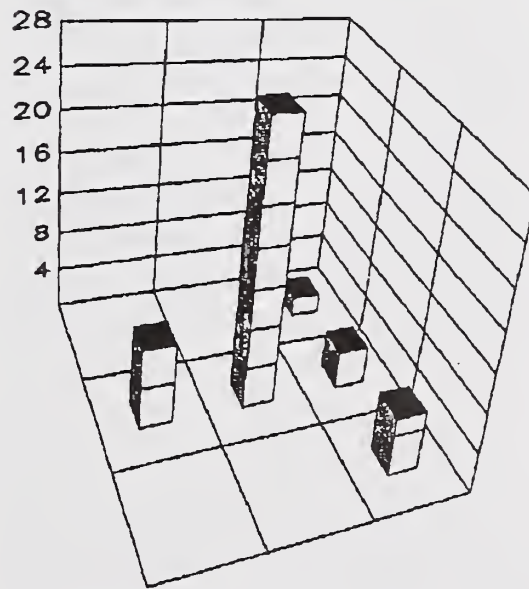
Taricha granulosa



Ensatina eschscholtzi



Rana aurora



Ascaphus truei

MEAN TOTAL CAPTURES

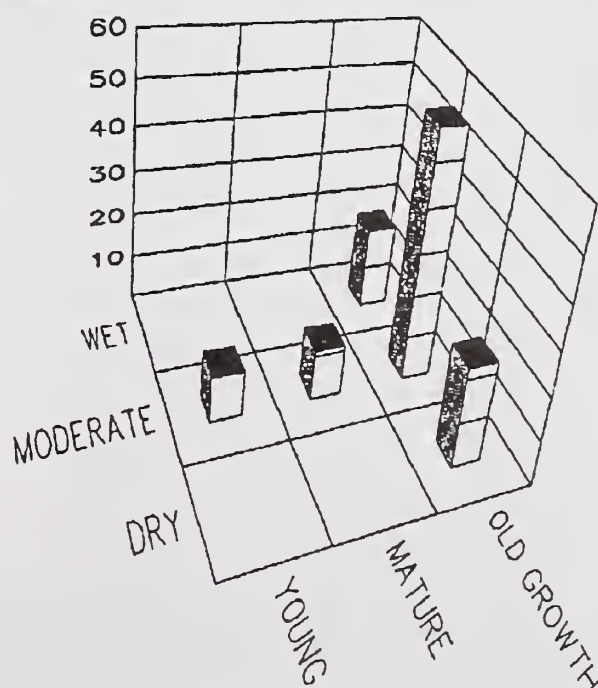


Figure 5.—Mean abundance of rough-skinned newts, northwestern salamanders, tailed frogs, red-legged frogs, and Oregon ensatinas in closed-canopy forest stands.

downed woody debris and the best-known method to sample such material is with TCS, area-constrained searches (Bury and Raphael 1983, Raphael and Rosenberg 1983), or hand-collecting of specific amounts and types of CWD.

For several reasons, we refrained from using TCS to compare differences in herpetofauna across stand ages and moisture gradients. In 1983, we did not record the number nor amount of litter (CWD) searched in each study site, which could have affected the results. Unless cover items are scarce, TCS will result in equivalent numbers of cover items searched, e.g., 20 logs per person-hr of search. However, the type, number and biomass of logs differs among stands. Thus, the number of animals collected is not related to the availability of cover (Corn and Bury unpublished data).

On the other hand, sites with large amounts of CWD may be occupied by many individuals yet few are revealed because they are dispersed. Douglas-fir forests can have over 1600 m³/ha of CWD (Spies et al. *in press*). Recently, we found that the density of salamanders in the Oregon Coast Range (number/m³ of CWD) was inversely related to the amount of CWD present in the stand (Corn and Bury unpublished data). TCS will underestimate abundance in stands with large amounts of CWD relative to stands with less CWD. Underestimation of the numbers of amphibians and reptiles in ecosystems is often more common than overestimation. Furthermore, we discovered that some collectors tended to focus on older decay classes of CWD (that often yield the highest catch) rather than uniformly searching all objects.

To estimate abundance of salamanders, we suggest recording the volume of CWD searched, control for time per object (e.g., 15 minutes maximum), balance effort (e.g., equivalent search between different decay classes of CWD), and relate

catch per volume of objects to separate estimates of the total CWD per hectare. These changes are needed to improve the value of TCS techniques for sampling the herpetofauna of forest ecosystems.

Pitfall traps catch the large numbers of individuals needed for quantified analyses of differences between forest stand types. They proved to be particularly important for sampling migratory species of amphibians, which we found to be common in Cascade forests. Also, our recent results indicate for the first time that tailed frogs occur in "upland" forested habitats.

Vogt and Hine (1982) pointed out that pitfall traps were most efficient during periods of precipitation or soon thereafter. Our results confirm these observations and, lately, we have reduced pitfall operations to 30-50 days in the fall only. Also, the triad design used here was highly effective but required great effort (900 m of drift fence was installed) in Pacific Northwest forests, which have large tree roots and rocky soils. Drift fences are more cost-effective in sandy areas where they can be more readily installed.

We caught few reptiles in the Cascade Mountains and pitfall traps were ineffective for these animals, even in the warmer summer months. Reptiles may be numerous in certain clearcuts (e.g., tables 4-5), in drier regions such as interior areas of northern California (e.g., Raphael and Barrett 1984, Raphael, this volume) and, based on our prior experience, in some young managed stands (10-30 years old). When present, these would be worth sampling with pitfall traps.

Pitfall traps alone are adequate to capture most amphibians and small mammals (Bury and Corn 1987) but overall sample size can be improved by increasing the number of traps per site. Thus, we have more recently employed a 6 by 6 pitfall grid (36 traps; 15-m spacing) and the catch is large enough for quantitative analy-

ses. These adjustments greatly increase the use and effectiveness of pitfall trapping in the Pacific Northwest and, likely, in other forested habitats.

Association of Herpetofauna with Old-Growth Forests

TCS revealed microhabitat differences between terrestrial species of salamanders, confirming general observations about these species (e.g., see Nussbaum et al. 1983, Stebbins 1985). However, the habitat requirements of these forms need better investigation.

The Oregon slender salamander seems to be associated with coarse woody debris in older decay classes, which is a characteristic feature of old-growth forests. This species is endemic to the Oregon Cascades, occurring only in Douglas-fir and subalpine forests. Thus, timber harvest might affect populations of slender

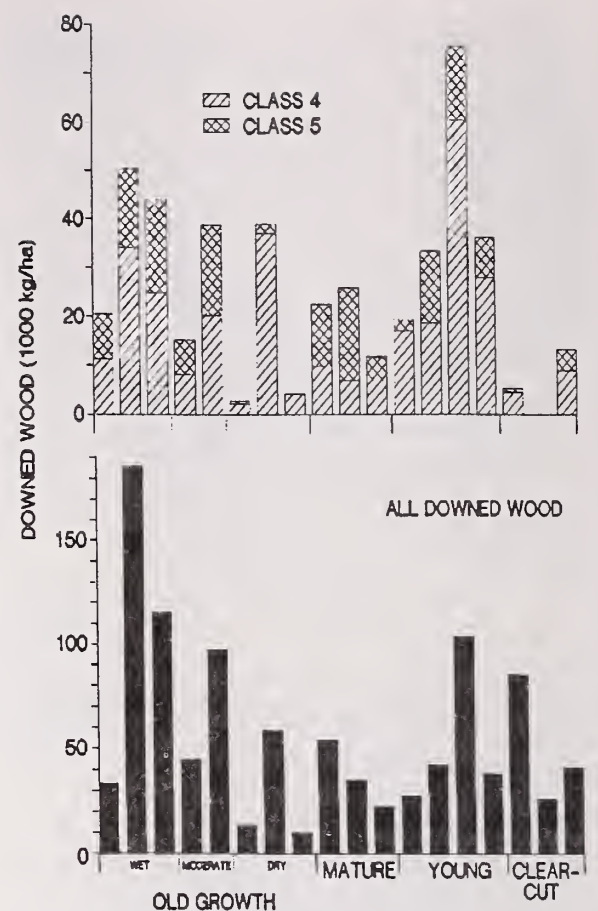


Figure 6.—Biomass of all (top) and class 4 and 5 (bottom) downed wood at 18 stands at the H. J. Andrews Experimental Forest, Oregon.

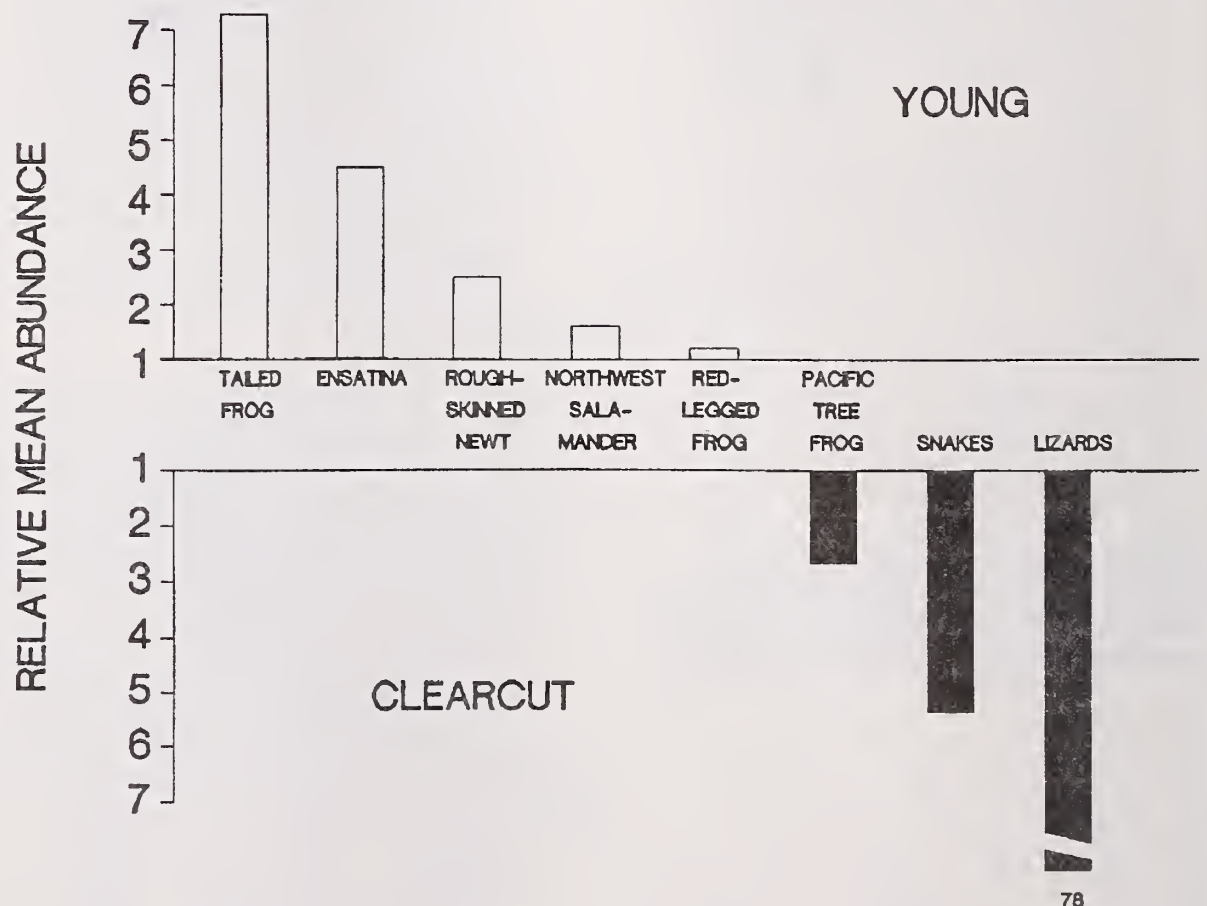


Figure 7.—Relative abundance of herpetofauna in young stands and clearcuts. Above the horizontal: species more abundant in young stands. Below: species more abundant in clearcuts. Values are the greater mean abundance divided by the lesser, e.g., lizards were 78 times more abundant in clearcuts than in young forest stands.

salamanders, and this species merits special study.

The Olympic salamander (*Rhyacotriton olympicus*) occurs in or near small streams, which can be disrupted by timber harvest (Bury 1988, Bury and Corn 1988, Welsh, this volume). Our techniques sampled terrestrial habitats and we found few of this species (pitfall traps took only 4 in old-growth and 1 in mature stands). Many tailed frogs were captured in pitfall traps in closed-canopy forests, but they were absent or rare in clearcuts (only 1% of the total catch). Both the Olympic salamander and the tailed frog seem to be sensitive to timber harvest, and the survival of these species may depend on protection of cool, flowing streams (required for breeding and larval development) as well as adjacent forested habitats (for shade and retention of stream substrate quality, see Bury and Corn 1988). There is a need to assess the effects of logging in streamside and upland forests, which may directly or indirectly affect amphibians in headwaters and small streams (Cooper et al. 1988, Bury and Corn 1988).

Adults of the rough-skinned newt and Northwestern salamander migrate to ponds for breeding and, later, the adults and juveniles move back to land, which obfuscates their relation to forest type. The red-legged frog breeds in slow-moving creeks or ponds, and the proximity of such waters may have influenced the abundance of the frog in adjacent stands.

Tailed frogs breed in small streams and the location of these waters can greatly influence the occurrence of the species in nearby forest stands. Also, we captured some juvenile and adult tailed frogs 100 to >300 m from the nearest stream (Bury 1988). Before our study, tailed frogs were not thought to move far from water (Metter 1964, Nussbaum et al. 1983). Proximity of aquatic breeding sites apparently influenced the capture of several species in up-

land habitat. At the same time, aquatic and semi-aquatic species might depend on the forest habitat for part of their life history, e.g., dispersal. We suggest that future research emphasize the life history requirements and movement patterns of amphibians, which might help to resolve which factors are most important to their continued local occurrence and abundance.

Fewer Oregon ensatina were captured in mature forests than either young or old-growth stands, and this salamander might be associated with large amounts of CWD in the Oregon Cascades. Mature forests lack input from large trees and snags (see discussions by Franklin et al. 1981, Harmon et al. 1986, Spies et al. *in press*). Disturbance (fire or blow-down) creates new young stands with appreciable amounts of CWD.

Similar to our results, Raphael and Barrett (1984) found that the abundance of Oregon ensatina in northern California was correlated to density of large Douglas-fir trees. However, they found few ensatina in the youngest stands (<150 years) they studied, and they included ensatina with species associated with old-growth stands. In the Oregon Cascades, ensatina were ubiquitous and there is no apparent correlation with old-growth stands.

Clouded salamanders were most abundant under the bark of relatively young logs. They may prefer class 2 and 3 logs, particularly occupying logs with loose bark. Also, clouded salamanders appear to be common in clearcuts (table 1). This species does not appear to be associated with old-growth conditions.

In Washington, we only found the Larch Mountain salamander (*Plethodon larselli*) at one old-growth stand (table 2). This species may be associated with forested stands (Herrington and Larson 1985), but the relation needs further inquiry and verification.

Management Considerations

Current evidence suggests that rich, abundant populations of herpetofauna occur in naturally regenerated forests. Within these stands, however, we found few differences in amphibians between wet, moderate, and dry old-growth sites and between young, mature, and old-growth stands. These results might be related to "old-growth" features occurring in many or all of these stands. For example, young and mature sites retained many characteristics of old-growth forests: complex structure, snags, and large amounts of downed woody debris, particularly in older decay classes (fig. 6). Such material is the result of wildfire that burns and kills larger trees, which later fall to the ground.

Wildfire often burns unevenly through stands, resulting in patches of lightly burned or unburned vegetation surrounded by areas more intensively affected by fire. Some large trees might not be killed during fires and these persist into the regenerated stand. Burned trees become snags that later fall to the forest floor, creating huge amounts of CWD. This heterogeneity and large amounts of CWD in naturally regenerated forest likely maintain favorable conditions for many species of the herpetofauna.

Managed stands (clearcuts) had little downed CWD in older decay classes (fig. 6) and, generally, no snags nor trees (except for a rare spar pole or small planted trees). Current forestry practices usually fell all trees and snags at sites, eliminating variability in stand age and structure. Logging is generally followed by prescribed burning of slash and cull logs, reducing CWD by 50% or more (Bartels et al. 1985, Maser et al. 1979). The large amount of CWD at one of our Oregon clearcuts reflects light burning (fig. 6). Also, this site was surrounded by dense, old-growth forest, which probably contributed large amounts of CWD before burning.

Often, the result of current timber harvest is even-aged stands with little CWD, especially in larger sizes. Present logging differs from that performed 30 or more years ago, when more CWD was left on the forest floor and smaller trees were left intact or ignored. Also, earlier practices tended to harvest larger, more valuable trees with little or no site preparation (except tree-planting), particularly on private lands. These were economic decisions, but the resultant second-growth stands may differ markedly from current intensive management of forests.

In contrast to clearcuts, young stands (naturally regenerated) we studied were closed-canopy and had much downed woody debris. The predominant species were the tailed frog and ensatina, and young stands had more newts, Northwestern salamanders and red-legged frogs than did clearcuts (fig. 7). Thus, there seem to be major differences in the herpetofaunas of pre-canopy clearcuts and naturally regenerated stands (young to old-growth).

There is a critical need to compare differences in wildlife in intensively managed stands and those subjected to other treatments (e.g., prior logging practices, select-cut). At this time, there is a lack of information on herpetofaunas or other wildlife in managed second-growth forests. Managed forests soon will be the predominate forest type in the Pacific Northwest and the bulk of our wildlife probably will occur in these stands. Wise management of these forests should be of foremost concern for wildlife managers, and done in concert with protection of isolated habitat patches (old-growth forest).

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Long-Term Trends in Abundance of Amphibians, Reptiles, and Mammals in Douglas-Fir Forests of Northwestern California¹

Martin G. Raphael²

Management of old-growth Douglas-fir (*Pseudotsuga menziesii*) forests is controversial in the Pacific Northwest, primarily because of the possible value of old-growth as habitat for certain wildlife species versus the revenues represented by old-growth trees (Meslow et al. 1981, Harris et al. 1982). Management to provide wildlife habitat requires an inventory of associated wildlife species and an assessment of their old-growth dependency. An analysis of the size and distribution of habitat patches necessary to support viable populations of those species is also critical (Burgess and Sharp 1981, Rosenberg and Raphael 1986, Scott et al. 1987).

This study describes the relative abundance of amphibians, reptiles, and mammals in six seral stages representing clearcuts, young timber stands, and mature forest in northwestern California. These estimates of relative abundance were used to project probable long-term changes in population size of amphibians, reptiles, and mammals as each seral

stage responds to forest management practices.

METHODS

Stand Selection

Study stands were on the Six Rivers, Klamath, and Shasta-Trinity National Forests within a 50-km radius of Willow Creek, Calif. Forest cover was dominated by Douglas-fir, usually in association with an understory of tanoak (*Lithocarpus ensiflorus*) and Pacific madrone (*Arbutus menziesii*). Elevations varied from 400 to 1300 m.

Abstract.—Relative abundance of 55 species of amphibians, reptiles, and mammals was estimated at 166 sites representing early clearcut through old-growth Douglas-fir forest in northwestern California. Nine species were strongly associated with older stands and 11 species were strongly associated with younger stands. The remaining species were either too rare to analyze statistically (22 species) or exhibited no clear trends of abundance in relation to stand age (13 species). Estimates of relative abundance of each species in each stage, coupled with data on historical, present, and future acreage of timber in each seral stage, were used to approximate the long-term impacts of timber harvest on the fauna of the Douglas-fir region in northwestern California.

The study region is characterized by warm, dry summers and cool, wet winters; total precipitation averages 60-170 cm per year.

After selecting potential study stands using timber maps and aerial photographs, I then located all stands that were accessible by road, were relatively homogeneous with respect to tree cover, included no large clearings or other anomalous features, and were free from scheduled timber harvest for at least the next 3 years.

From this restricted subset of stands, I randomly chose 10 to 15 stands representing each of six seral stages:

Stage	Seral state	Age (yrs)	Classification
1	Early	<10	Clearcut (brush/sapling)
2	Late	10-20	
3	Pole	20-50	
4	Sawtimber	50-150	Young forest (pole/sawtimber)
5	Mature	150-250	
6	Old-growth	>250	Mature forest

Raphael and Barrett (1984) describe methods for aging these stands. Ground surveys were used to verify stand conditions. Forest Service stand designations were used to guide stand selection, but the final classification of each stand into seral stages was based on measured vegetation characteristics.

Vegetation Sampling

The structure and composition of vegetation on each stand in the three older seral stages was measured in three, randomly selected, 0.04-ha circular subplots within a 90-m radius of each plot center. Within each subplot, observers recorded species,

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height, diameter at breast height (d.b.h.) and crown dimensions of each tree or shrub >2.0 m tall. In addition, all trees >90-cm d.b.h. were counted on one 0.50-ha circular subplot centered on the plot. This sample permitted a better estimate of the density of large-diameter trees. Numbers of larger (>8-cm diameter) logs and volume of other downed woody debris were estimated along a 30-m transect crossing the center of each 0.04-ha subplot (Brown 1974). Marcot (1984) sampled vegetation in a similar manner on stands in the three early-seral stages.

Vertebrate Sampling

All field data were collected by a team of three to six biologists. We used a variety of techniques to sample various taxonomic groups.

Pitfall Arrays

We used pitfall arrays to capture small mammals (especially insectivores), reptiles, and salamanders. An array was composed of ten 2-gallon plastic buckets buried flush with the ground and covered with plywood lids, arranged in a 2 x 5 grid with 20-m spacing. We placed one array within each stand center and checked traps at weekly to monthly intervals from December 1981 (sawtimber, mature, old-growth; $n = 27, 56$, and 52 sites in each stage, respectively) or August 1982 (early shrub-sapling, late shrub-sapling, pole; $n = 10$ sites each) until October 1983. All live animals were marked and released; recaptures were excluded from analyses. Dead animals were collected and prepared for permanent deposit in museum collections. Results for each species were expressed as captures per 1000 trapnights on each stand. Raphael and Rosenberg (1983) demonstrated that abundance estimates (capture rates) had stabilized after 15 months of continuous trapping.

Drift Fence Arrays

To better sample snakes, we installed a drift fence array (Campbell and Christman 1982, Vogt and Hine 1982) on each of 60 randomly selected stands (10 of each of the three early stages and sawtimber, 8 mature, and 12 old-growth). An array consisted of two 5-gallon buckets placed 7.6 m apart and connected by an aluminum fence 7.6 m long and 50 cm tall with two 20 x 76 cm cylindrical funnel traps, one on each side of the center of the fence. These fences were operated from May through September 1983. All captures were combined with those from the pitfall arrays along with the associated trapnights from each stand.

Track Stations

Tracks of squirrels and other larger mammals were recorded on each site on a smoked aluminum plate baited with tuna pet food (Barrett 1983, Raphael and Barrett 1981, Raphael et al. 1986, Taylor and Raphael 1988). Based on results of a pilot study (Raphael and Barrett 1981), observers monitored each station for 8 days in August or September in 1981-1983, sampling 20 stations in each of the three early stages and 81, 168, and 157 stations in the sawtimber, mature, and old-growth stages, respectively. The proportion of stations in each seral stage on which a species occurred was as an index of that species' abundance.

Livetrapping Grids

To better estimate abundance of small mammals that were liable to escape from pitfalls, we established 27 livetrapping grids (3 in each of the three earliest stages and 5, 7, and 6 in the three later stages), each of which usually consisted of 100 25-cm Sherman livetraps arranged in a 10 x 10 grid with 20-m spacing. Other grid

sizes or shapes were used when the plot configuration would not contain the standard grid. Traps were checked each day for 5 days (based on pilot studies, Raphael and Barrett 1981) during July in 1981 (late stages only), 1982, and 1983 (all stages). Results for each species were expressed as mean number of captures per 100 trapnights.

Surface Search

To better sample certain amphibian species, we conducted time- and area-constrained searches (Bury and Raphael 1983, Raphael 1984) on a subset of sites in 1981 (late stages), 1982, and 1983 (all stages). A two-person team searched under all movable objects and within logs on three randomly located 0.04-ha circular subplots (fall 1981, 1982) or within a 1-ha area for 4 working hours (spring 1983). We conducted 20 surveys in each of the three early stages and 29, 39, and 48 surveys in the three late stages.

Opportunistic Observations

Observers recorded the presence of vertebrates or identifiable vertebrate sign incidental to the above procedures. We tallied observations to calculate frequency of occurrence of rarer species within each stage.

Forest Area Trends

Estimates of historical, current, and future acreage in each seral stage were taken from Raphael et al. (in press). For these analyses, I combined similar pairs of seral stages into three generalized stages representing brush/sapling, pole/sawtimber, and mature timber. I then computed relative abundance of each vertebrate species in these three stages using a weighted average (weights based on sampling effort) of

estimates from each of the two stages forming the pair. Population estimates for historical, present, and future time periods were computed using the formula:

$$P_{it} = \sum_{j=1}^3 D_{ij} A_{jt}$$

where P_{it} was the relative population size of the i th vertebrate species at time t , D_{ij} was the relative abundance of the i th vertebrate in the j th seral stage, and A_{jt} was the total area of each of the three seral stages at time t .

RESULTS

Vegetation Structure

Comparisons of vegetation structure among the seral stages (table 1) showed that older stands had greater

canopy volume, basal area, litter depth, and density of Douglas-fir stems >90 cm d.b.h. Downed wood mass differed among stages, but the greatest volume occurred in the youngest stands, probably in the form of logging slash, and the lowest volume occurred in pole and sawtimber stages. Early-seral stands were higher in elevation than older stands, probably because of the logistics of timber harvest in the area (most clearcuts were located along ridgetops). Stands in the two earliest seral stages, also because of logging, were smaller in area than stands in the four older stages.

Vertebrate Abundance and Diversity

Among all plots and years of study, we recorded 9,928 captures of all

species during 898,431 trapnights from pitfalls and drift fences; 1,636 captures of amphibians during surface searches; 3,066 small mammal captures during 35,070 trapnights from livetraps grids; and 510 detections of larger mammals from track stations. Relative abundances of 55 species, based on the most appropriate sampling method for each species, are summarized in table 2. Values are comparable across stages but not among taxa if different sampling methods were used. Amphibians were much more abundant in forested than in clearcut stands, whereas reptiles were more abundant in clearcuts. None of the amphibians and reptiles [except rarer species such as northwestern salamander (see appendix for scientific names of vertebrates)] was absent from any stage.

Mammals exhibited a greater variety of responses to seral stage. Some (e.g., Douglas' squirrel, western red-backed vole) increased in abundance from earliest to latest seral stages; others (e.g., deer mouse) decreased along this gradient. A number of species (e.g., Allen's chipmunk, dusky-footed woodrat, pinyon mouse, California vole) were most abundant both in late shrub-sapling and mature or old-growth stands.

Mean numbers of mammal and reptile species recorded per stand differed among seral stages, but mean numbers of amphibian species did not differ significantly (fig. 1). Among mammals, mean numbers of species were greatest in mature and old-growth stages. In contrast, mean numbers of reptile species were greatest in the two earliest stages.

Long-Term Trends

Estimates of land area in each seral stage through time (table 3) indicate more area is occupied by early seral stages currently than during historic or future times. Mature and old-growth stages currently occupy

Table 1.—Comparisons of vegetation characteristics among seral stages of Douglas-fir forest, northwestern California, 1981-1983.

Characteristic	Early brush/sapling	Late brush/sapling	Pole	Sawtimber	Mature	Old-growth
Canopy volume (m ³ /m ²)	¹ 0.77	¹ 1.26	¹ 3.64	7.15	7.52	7.47
Live stem basal area (m ² /ha)	¹ 0.9	¹ 2.6	¹ 52.8	50.5	60.2	65.6
Snag basal area (m ² /ha)	² —	—	¹ 11.1	4.7	6.1	5.3
Downed wood mass (metric tons/ha)						
<8 cm diameter	¹ 9.7	¹ 7.9	¹ 11.9	12.9	12.3	11.5
≥8 cm diameter	¹ 81.4	¹ 74.7	¹ 52.4	32.3	43.6	67.3
Litter depth (cm)	¹ 2.2	¹ 4.8	¹ 6.0	6.2	5.1	7.1
Douglas-fir >90 cm d.b.h. (n/ha)	—	—	—	3.6	19.3	25.7
Elevation (m)	1128	1016	972	660	832	904
Stand area (ha)	12.3	21.9	41.2	47.1	62.0	84.2
Solar radiation index ³	0.34	0.41	0.51	0.49	0.49	0.43
Slope (%)	48	30	31	36	41	52
Age (years since clearcut, or index)	9	14	—	123	206	294

¹Data are from Marcot (1984), with permission, and represent a larger number of sites than were sampled in the present study.

²Dashes indicate no values were available.

³Index of total yearly solar energy flux (Frank and Lee 1966). Larger values indicate warmer, drier sites.

Table 2.—Mean relative abundance of amphibians, reptiles, and mammals among seral stages of Douglas-fir forest, northwestern California, 1981-1983.

Species ¹	Sampling method(s) ²	Total captures	Relative abundance among seral stages ³					Significance ⁴	
			1	2	3	4	5		
Salamanders									
Northwestern salamander ⁵	PD, TC ⁶	6	0	0	0	1	3	4	—
Pacific giant salamander	PD	28	0	0.05	0	0.01	0.02	0.04	0.114
Olympic salamander ⁵	PD, TC ⁶	5	0	0	0	1	1	3	—
Rough-skinned newt	PD	68	0.02	0	0	0.05	0.09	0.04	0.403
Del Norte salamander	TC	196	0.70	0.60	0.05	0.07	1.92	1.92	0.035
Ensatina	TC	1116	2.40	1.85	8.10	6.28	8.15	7.69	0.001
Black salamander	TC	32	0.05	0.05	0.05	0.03	0.21	0.42	0.011
Clouded salamander	TC	103	0.35	1.55	0.50	0.10	0.31	0.83	0.009
Frogs and toads									
Tailed frog ⁵	PD, TC ⁶	3	0	0	0	0	2	0	—
Western toad	PD	54	0.18	0.03	0.02	0.08	0.06	0.01	0.035
Pacific treefrog	TC	51	0.60	0.05	0.10	0.55	0.03	0.06	0.000
Foothill yellow-legged frog ⁵	TC ⁴	6	1	0	0	1	0	0	—
Bullfrog ⁵	OO ⁴	3	0	0	0	1	0	0	—
Turtles									
Western pond turtle ⁵	OO ⁶	5	0	0	0	4	0	0	—
Lizards									
Western fence lizard	PD	523	1.77	2.38	0.30	0.94	0.54	0.11	0.000
Sagebrush lizard	PD	196	2.66	0.76	0.25	0.09	0.11	0.01	0.000
Western skink	PD	584	3.05	3.47	0.78	0.73	0.42	0.13	0.000
Southern alligator lizard	PD	41	0.03	0	0	0.11	0.05	0.03	0.085
Northern alligator lizard	PD	586	0.81	1.03	0.90	0.97	0.60	0.44	0.029
Snakes									
Rubber boa ⁵	OO, PD ⁶	7	0	20	10	0	4	0	—
Ringneck snake ⁵	OO, PD ⁶	6	0	0	0	0	4	0	—
Sharp-tailed snake ⁵	PD ⁴	22	10	20	30	0	5	4	—
Racer ⁵	OO, PD ⁶	8	0	20	0	4	5	4	—
Gopher snake ⁵	OO, PD ⁶	3	0	0	10	0	2	0	—
Common kingsnake ⁵	OO, PD ⁶	1	0	0	0	4	0	0	—
Common gartersnake ⁵	OO, PD ⁶	19	20	10	20	0	5	11	—
Western terrestrial gartersnake ⁵	4OO, PD	11	0	20	10	7	4	6	—
Western rattlesnake ⁵	OO, PD, TC ⁶	5	0	10	0	0	2	6	—
Mammals									
Pacific shrew	PD	89	0.02	0.08	0	0.07	0.07	0.17	0.004
Trowbridge's shrew	PD	2384	2.70	4.01	2.83	3.04	3.16	3.80	0.215
Shrew-mole	PD	479	0.04	0.16	0.25	0.76	0.55	0.55	0.002
Coast mole ⁵	PD	15	0	0.03	0	0.02	0.05	0.06	—
Allen's chipmunk	LT	254	16.7	29.5	0.8	2.8	5.2	5.0	0.003
Western gray squirrel	TP ⁴	48	0	0	10	12	12	9	0.378
Douglas' squirrel	TP ⁴	104	0	0	20	16	22	30	0.001
Northern flying squirrel	TP ⁴	43	0	0	15	9	18	13	0.046

(continued)

Table 2.—(continued).

Species ¹	Sampling method(s) ²	Total captures	Relative abundance among seral stages ³						Significance ⁴
			1	2	3	4	5	6	
Deer mouse	PD	1127	5.09	3.07	0.39	0.58	0.98	1.28	0.000
Brush mouse	LT	33	0	0.33	3.67	0.25	0.25	0	0.216
Pinyon mouse	LT	222	1.35	10.34	4.67	10.63	3.86	2.76	0.086
Dusky-footed woodrat	LT	115	1.9	3.5	0.2	1.2	4.4	3.4	0.000
Western red-backed vole	PD	669	0.35	0.36	0.46	0.45	0.82	0.97	0.015
Red tree vole	PD	19	0	0.10	0	0.07	0.11	0.15	0.586
California vole	PD	106	0.89	1.70	0.03	0.02	0.01	0.01	0.000
Creeping vole	PD	22	0.09	0.03	0.05	0.04	0.01	0.01	0.038
Western jumping mouse ⁵	PD	2	0	0	0	0	0.04	0.02	—
Coyote ⁵	ALL ⁶	7	10	30	0	15	9	15	—
Gray fox	TP ⁶	63	20	15	10	30	11	8	0.001
Black bear	TP ⁶	196	20	25	5	42	45	48	0.028
Ringtail	TP ⁶	25	0	0	0	10	6	4	0.249
Raccoon ⁵	TP ⁶	3	0	0	0	0	1	1	—
Fisher	TP ⁶	58	0	5	25	6	13	15	0.060
Ermine ⁵	PD	2	0	0	0	0	0.02	0.02	—
Western spotted skunk	TP ⁶	70	10	15	5	10	18	15	0.426
Striped skunk ⁵	TP ⁶	17	0	0	0	7	6	1	—
Bobcat ⁵	TP ⁶	3	5	5	0	1	2	0	—

¹All names follow Laudenslayer and Grenfell (1983).

²PD = Pitfall plus drift fence, TC = Time- and area-constrained search, OO = Opportunistic observations, TP = Track plots, LT = Live traps, ALL = all observation methods combined.

³Seral stages (and numbers of stands sampled) are: 1—early brush/sapling (n=10); 2—late brush/sapling (n=10); 3—pole (n=10); 4—sawtimber (n=27); mature (n=56); 5—old-growth (n=53).

⁴Significance from analysis of variance (means) or chi-square analysis (frequencies) comparing abundances among stages. A dash indicates that no test was performed.

⁵Too rare for subsequent analyses.

⁶Abundance values based on percent frequencies.

about half of historic acreage, and these stages will probably occupy only about 30% of current acreage under the most likely harvest patterns of the future (table 3).

The implications of these changing distributions of seral stages for amphibians, reptiles, and mammals are summarized in figure 2. Nearly equal numbers of species are likely to have increased or decreased by more than 25% relative to historic abundance at present and in the future. Three of the five reptile species are presently more abundant than in historic times and all five species will likely be more abundant in the future. Amphibians showed an opposite pattern.

Four of the eight species are presently less abundant and five of the eight may be less abundant in the future. Among the 20 mammal species, seven are presently less abundant than in historic times whereas five are more abundant. Eight species will probably be less abundant in the future and six more abundant.

DISCUSSION

Abundance in Seral Stages

Results suggest late brush/sapling and mature/old-growth seral stages provided more productive wildlife

habitat than early brush/sapling, pole, and sawtimber stages. Among amphibians, only ensatinas were captured frequently in pole sites. Clouded salamanders were generally under bark or inside downed logs and persisted in clearcut stands as long as adequate numbers of logs were retained, especially in late sites (Raphael 1987, Welsh, this volume).

Lizards were more abundant in earlier seral stages than in pole and mature stages. Among snakes, only sharp-tailed snakes were observed on early sites; other species occurred on later sites. However, sampling was not sufficient for definitive conclusions.

With the exception of the deer mouse, small mammals were more abundant on late brush/sapling sites. Dusky-footed woodrats were of special interest in this regard as we observed many woodrat nests built among the stems of tanoak and Pacific madrone in late brush/sapling sites. The combination of abundant mast, good nesting substrate, and protection from predation (spotted owls rarely forage in old, brush-dominated clearcuts) provided by the dense, brushy cover were probably the reasons that woodrats and other small mammals were more numerous in late clearcut sites (Raphael 1987).

Tree squirrels were most abundant in mature forest sites and ground squirrels were more abundant in early clearcut sites. Chipmunks were the only squirrel that reached peak abundance in early seral sites. Their abundance was correlated with the cover of tanoak in the understory (Raphael 1987). Management actions, such as herbicide treatments, that shorten or delete the late brush/sapling stage are probably detrimental to chipmunks, woodrats, and certain other rodents.

Several carnivorous mammals were abundant in the late brush/sapling stage. Greater prey density in late compared to early and pole sites may explain this higher frequency of carnivores although more data will be necessary to confirm this observation.

Of the 55 species observed, 20 were strongly associated with either older (9 species) or younger (11 species) stands (table 4). Three salamanders and six mammals were associated with older stands. One toad, one frog, five lizards, and four mammals were associated with younger stands. Five species associated with old-growth were also abundant in late (brushy) clearcut stages (table 2). These species peak in abundance in old stands and late clearcuts, with low abundance in intermediate age classes.

Table 3.—Approximate area (millions of ha) of seral stages in Douglas-fir forests of northwestern California in historic, present, and future time periods (after Raphael et al., in press).

Seral stage	Historical	Present	Likely future	Worst case future ¹
Brush/sapling	0.14	0.49	0.20	0.24
Young forest	0.14	0.20	0.77	0.85
Mature forest	0.81	0.40	0.12	0.00

¹Assumes that all mature and old-growth stands are harvested and all lands managed under short rotations.

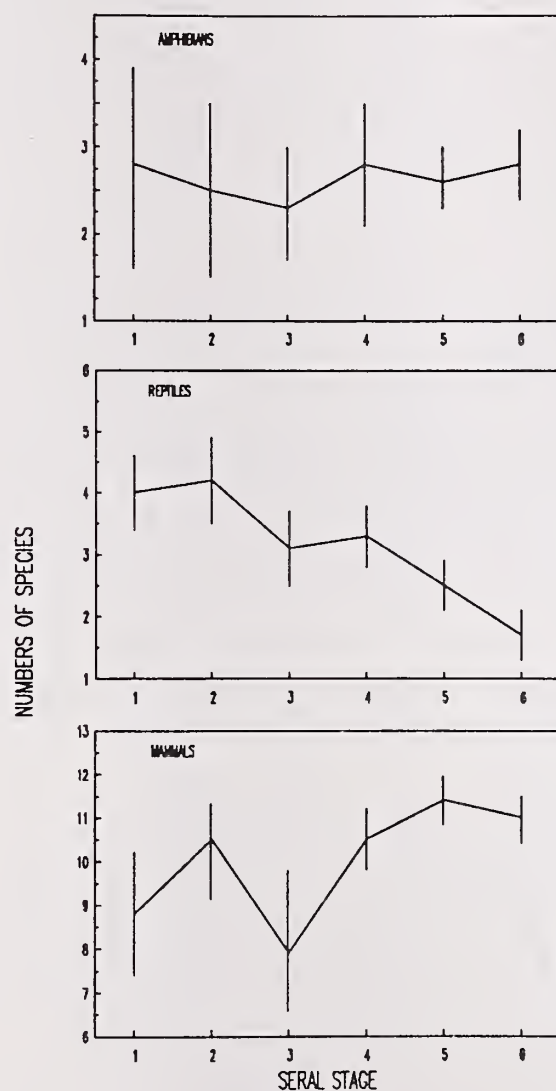


Figure 1.—Mean numbers of amphibian, reptile, and mammal species observed in seral stages of Douglas-fir forest, northwestern California, 1981-1983. Seral stages (and numbers of stands sampled) are: 1 - early brush/sapling ($n = 10$); 2 - late brush/sapling ($n = 10$); 3 - pole ($n = 10$); 4 - sawtimber ($n = 27$); 5 - mature ($n = 56$); 6 - old-growth ($n = 53$). Vertical lines indicate 95% confidence intervals.

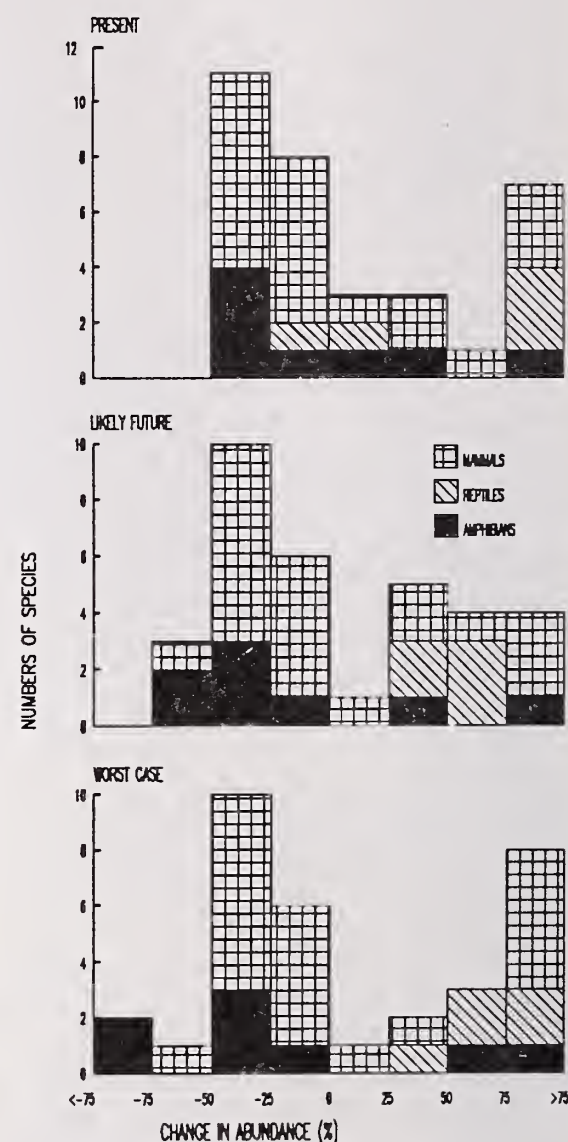


Figure 2.—Percent change in population size of amphibian, reptile, and mammal species at present and in the future relative to estimated historical populations. Histograms represent the numbers of species increasing or decreasing by specified percentages.

I examined habitat associations among each of the above 9 species by computing correlations of their abundance with specific habitat components (table 5). Density of large trees and hardwood volume were correlated with the abundance of most species. Moisture, as measured by the presence of surface water, moisture-loving tree species, or north-facing slopes, was important for most mammals and one salamander species. Four mammal species were significantly more abundant on higher elevation stands. Downed wood volume also was significantly and positively correlated with abundance of four amphibian and mammal species. The abundance of hardwoods in the understory was important for many species in each group. In contrast, snag density was not positively correlated with the abundance of any species.

Long-Term Trends

The list of sensitive species (table 4) is tentative pending results of addi-

Table 5.—Habitat components that were correlated with relative abundance of amphibians and mammals associated with late-seral Douglas-fir forests of northwestern California.

Species	Density of conifers >90-cm d.b.h.	Hardwood under- story	Downed wood mass	Standing snags	Moisture	Elevation
Del Norte salamander		X				
Black salamander		X			X	
Clouded salamander	X		X			
Pacific shrew	X		X		X	X
Douglas' squirrel	X	¹ (X)	X		X	X
Northern flying squirrel		X				(X)
Dusky footed woodrat	X	X			X	X
Western red-backed vole	X		X		X	X
Fisher	X	X				

¹Parentheses indicate negative correlations.

tional surveys and more intensive, species-specific research. The projections, although based on an intensive sampling effort, are highly speculative. Three assumptions must be recognized to interpret these results. First, I assumed that greater relative abundance in a seral stage indicates a species' preference for that stage and that preferences remain constant with shifting distribution of acreage

in each stage. Some species have (or could) adapt to new stages over time.

Second, I assumed total acreage of each seral stage can be used to estimate responses of vertebrates without regard to size and juxtaposition of stands comprising each stage. However, continued fragmentation of forest habitats may result in disjunct patches so small they cannot support a species that would otherwise find the habitat suitable. Rosenberg and Raphael (1986) found that at least eight species of amphibians (2), reptiles (2), and mammals (4) were significantly less abundant in stands <10 ha in size than in larger stands. Some of these (e.g., western gray squirrel) were not listed in this study among the sensitive species (table 4), but the effects of habitat fragmentation may nonetheless be cause for concern.

A third assumption is that young forested stands (pole, sawtimber) in this study represent young stands of the future. Naturally occurring pole and sawtimber stands contain some large Douglas-fir stems and a substantial amount of standing and downed wood (table 1). If future management activities result in fewer large live trees, snags, and downed logs, the abundance of vertebrates associated with these habitat components may also decline. In this case,

Table 4.—Amphibian, reptile, and mammal species most strongly affected by future harvest of old-growth Douglas-fir forest, northwestern California.¹

Decreasers—associated with late-seral forest		Increaseers—associated with early-seral forest	
Species	% decline ²	Species	% increase ²
Del Norte salamander	75	Western toad	45
Black salamander	71	Pacific treefrog	160
Clouded salamander	29	Western fence lizard	60
Pacific shrew	39	Sagebrush lizard	44
Douglas' squirrel	31	Western skink	59
Northern flying squirrel	31	Southern alligator lizard	60
Dusky-footed woodrat	55	Northern alligator lizard	43
Western red-backed vole	37	Pinyon mouse	70
Fisher	26	California vole	44
		Creeping vole	102
		Gray fox	78

¹Species were listed if their estimated future abundance differed by more than 25% from estimated historical abundance and if mean abundance differed significantly ($P < 0.10$) among seral stages (table 2).

²Percent increase or decrease in estimated future abundance compared with estimated historic abundance.

responses of vertebrates to forest management may be more extreme than those projected.

The overall trend is for increased abundance among species of southern affinity that are associated with open, drier habitats in other parts of their ranges, and decreased abundance among species of boreal affinity that are primarily associated with moist coniferous forest throughout their ranges. Furthermore, most of the increasers are widespread species with large distributions that include many nonthreatened habitats. In contrast, the decreasers are almost all species with rather restricted total ranges, most of which are in threatened habitats. Therefore, even though total numbers of increasers and decreasers are nearly equal, the effects of old-growth reduction should not be viewed as neutral.

Because many of the decreasers are affected by soil moisture and other microclimatic conditions, management to protect stream edges, moist ravines, and other moist sites may provide refuges for species that can later recolonize maturing stands. Management efforts to retain (or recreate) natural components of regenerating stands, such as hardwood understory, snags, and logs, may help mitigate against wildlife losses in future forests. It is not stand age, per se, but the structural characteristics of forests of various ages that are important to survival of most species.

Finally, results of this study address another important forest management issue in the northwest; What should managers use as a baseline for evaluation of impacts: historic or present conditions? It is apparent that many species are presently much less abundant compared with historic numbers (fig. 2). Additional reductions because of continued timber harvest will cause further declines in some species but most major declines have already occurred. Therefore, I believe that estimates of historic populations should

be used as baselines for monitoring biological diversity, rather than present populations.

ACKNOWLEDGMENTS

Field studies were funded by the Pacific Southwest Region and the Pacific Southwest Forest and Range Experiment Station of the USDA Forest Service and by the University of California, Agricultural Experiment Station 3501 MS. I especially thank my field assistants (Paul Barrett, John Brack, Cathy Brown, Christopher Canaday, Lawrence Jones, Ronald LaValley, Kenneth Rosenberg, and Cathy Taylor) for their dedication and blisters; R. H. Barrett, C. J. Ralph, and J. Verner for their support; Bruce G. Marcot for freely sharing information from his studies and for valuable discussions; and Kenneth V. Rosenberg, Fred B. Samson, and Hobart M. Smith for their comments on an earlier draft of this manuscript.

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Appendix

Common and scientific names of vertebrates mentioned in text (nomenclature follows Laudenslayer and Grenfell (1983)).

Salamanders

Northwestern salamander	<i>Ambystoma gracile</i>
Pacific giant salamander	<i>Dicamptodon ensatus</i>
Olympic salamander	<i>Rhyacotriton olympicus</i>
Rough-skinned newt	<i>Taricha granulosa</i>
Del Norte salamander	<i>Plethodon elongatus</i>
Ensatina	<i>Ensatina eschscholtzi</i>
Black salamander	<i>Aneides flavipunctatus</i>
Clouded salamander	<i>Aneides ferreus</i>

Frogs and toads

Tailed frog	<i>Ascaphus truei</i>
Western toad	<i>Bufo boreas</i>
Pacific treefrog	<i>Hyla regilla</i>
Foothill yellow-legged frog	<i>Rana boylei</i>
Bullfrog	<i>Rana catesbeiana</i>

Turtles

Western pond turtle	<i>Clemmys marmorata</i>
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Lizards

Western fence lizard	<i>Sceloporus occidentalis</i>
Sagebrush lizard	<i>Sceloporus graciosus</i>
Western skink	<i>Eumeces skiltonianus</i>
Southern alligator lizard	<i>Gerrhonotus multicarinatus</i>
Northern alligator lizard	<i>Gerrhonotus coeruleus</i>

Snakes

Rubber boa	<i>Charina bottae</i>
Ringneck snake	<i>Diadophis punctatus</i>
Sharp-tailed snake	<i>Phyllorhynchus decurtatus</i>
Racer	<i>Coluber constrictor</i>
Gopher snake	<i>Pituophis melanoleucus</i>
Common kingsnake	<i>Lampropeltis zonata</i>

Common gartersnake	<i>Thamnophis sirtalis</i>
Western terrestrial gartersnake	<i>Thamnophis elegans</i>
Western rattlesnake	<i>Crotalis viridis</i>

Mammals

Pacific shrew	<i>Sorex pacificus</i>
Trowbridge's shrew	<i>Sorex trowbridgii</i>
Shrew-mole	<i>Neurotrichus gibbsii</i>
Coast mole	<i>Scapanus orarius</i>
Allen's chipmunk	<i>Tamias senex</i>
Western gray squirrel	<i>Sciurus griseus</i>
Douglas' squirrel	<i>Tamiasciurus douglasii</i>
Northern flying squirrel	<i>Glaucomys sabrinus</i>
Deer mouse	<i>Peromyscus maniculatus</i>
Brush mouse	<i>Peromyscus boylii</i>
Pinyon mouse	<i>Peromyscus truei</i>
Dusky-footed woodrat	<i>Neotoma fuscipes</i>
Western red-backed vole	<i>Clethrionomys californicus</i>
Red tree vole	<i>Arborimus longicaudus</i>
California vole	<i>Microtus californicus</i>
Creeping vole	<i>Microtus oregoni</i>
Western jumping mouse	<i>Zapus princeps</i>
Coyote	<i>Canis latrans</i>
Gray fox	<i>Urocyon cinereoargenteus</i>
Black bear	<i>Ursus americanus</i>
Ringtail	<i>Bassariscus astutus</i>
Raccoon	<i>Procyon lotor</i>
Fisher	<i>Martes pennanti</i>
Ermine	<i>Mustela erminea</i>
Western spotted skunk	<i>Spilogale gracilis</i>
Striped skunk	<i>Mephitis mephitis</i>
Bobcat	<i>Lynx rufus</i>

Use of Woody Debris by Plethodontid Salamanders in Douglas-Fir Forests in Washington

Keith B. Aubry,¹ Lawrence L. C. Jones,² and
Patricia A. Hall³

The harvesting of old-growth Douglas-fir (*Pseudotsuga menziesii*) forests in the Pacific Northwest, and its potential effects on wildlife species has been the focus of much concern in recent years (e.g., Lumen and Nietro 1980, Franklin et al. 1981, Meslow et al. 1981, Meehan et al. 1984, Gutierrez and Carey 1985). Most of this attention has been directed towards birds and mammals such as the spotted owl (*Strix occidentalis*), Vaux's swift (*Chaetura vauxi*), northern flying squirrel (*Glaucomys sabrinus*), and red tree vole (*Arborimus longicaudus*); little concern has been expressed about amphibians and reptiles. These groups have not been studied extensively in the Pacific Northwest. Only recently has research been conducted on habitat associations among different forest age classes (Raphael 1984, Raphael and Barrett 1984, Ruggiero and Carey 1984).

From 1983 to 1986, the USDA Forest Service and USDI Bureau of Land

Management funded a major research effort aimed at identifying wildlife species that occur in highest abundances in old-growth Douglas-fir forests and investigating the ecological basis of observed patterns of association

Amphibian communities were sampled using pitfall traps, stream surveys, and time-constrained searches (Standard Sampling Protocols on file at the Forestry Sciences Laboratory, Olympia, WA). Some of the results of these studies are reported elsewhere in this volume (Bury and Corn 1988, Welsh 1988). Here, we report the results of time-constrained searches conducted in southern Washington in 1984. Our objectives are to (1) identify potential habitat associations, (2) examine patterns of cover object use, and (3) evaluate the efficacy of this technique for studying amphibians in this region.

Study Area

Forty-five forest stands were sampled in the southern portion of the Cascade Range in Washington (fig. 1). Stands ranged in age from 55 to 730 yr and were at least 20 ha in size. All stands were located within the western hemlock (*Tsuga heterophylla*) zone and lower elevations of the Pacific silver fir (*Abies amabilis*) zone (Franklin and Dyrness 1973), which are characterized by a wet and

Abstract.—*Ensatina eschscholtzii* was found most often under pieces of bark, whereas *Plethodon vehiculum* occurred primarily under logs. Captures of both species were highest in young stands, but occurred in all age classes. Our results suggest that the retention of coarse woody debris in managed forests would provide for the habitat needs of these species.

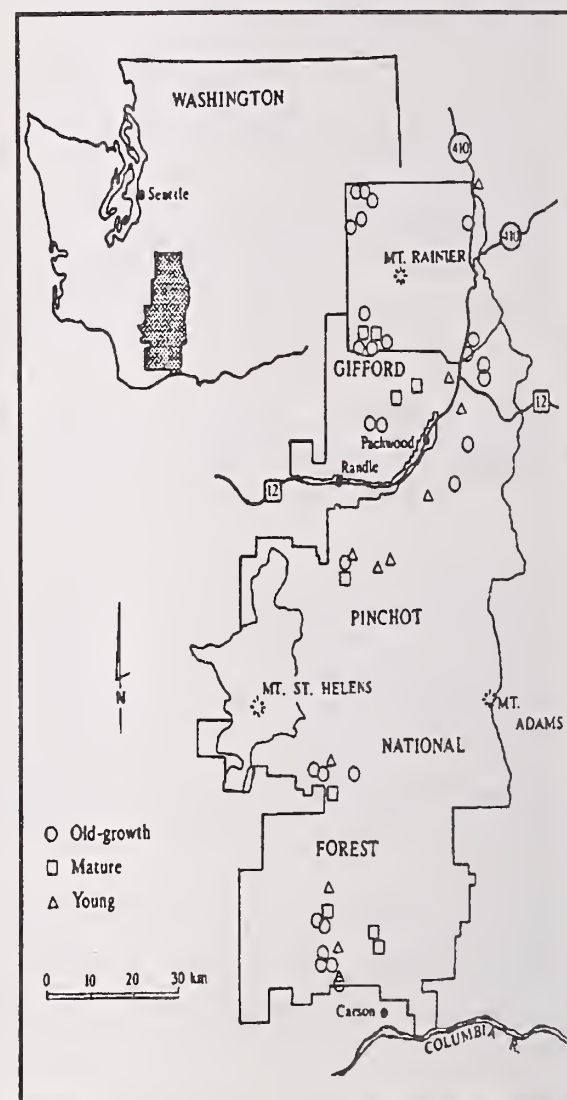


Figure 1.—Location of study stands by age class in the southern Washington Cascade Range.

mild maritime climate. Snow rarely accumulates at our sites.

Old-growth stands (210-730 yr) typically contained high proportions of Douglas-fir and western hemlock and, in wet sites, western redcedar (*Thuja plicata*). Mature (95-190 yr) and young (55-80 yr) stands were

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dominated by Douglas-fir. In all age classes, other species such as red alder (*Alnus rubra*), vine maple (*Acer circinatum*), bigleaf maple (*A. macrophyllum*), Pacific silver fir, and western hemlock occurred in lesser amounts.

Average age of each stand was determined through growth ring counts, either by increment coring or examination of cut stumps in nearby stands. Old-growth stands were classified into wet, moderate, and dry moisture classes on the basis of floristic and physiographic characteristics; all young and mature stands were in the moderate moisture class (T. A. Spies, unpubl. data). All stands had resulted from natural regeneration following fires; none had undergone silvicultural treatments.

Methods

Surveys for terrestrial amphibians were conducted from 16 April to 12 June 1984; all but four high-elevation stands were sampled by 4 May. A time-constrained search method was used (Campbell and Christman 1982). A crew of two to four persons actively searched each stand for amphibians for a total of 4 person-hours. An initial search area was selected at least 50 m within the stand to avoid edge effects.

In general, woody debris such as logs, snags, and pieces of bark was abundant in each stand and constituted virtually all potential cover objects. An area was searched for 0.5 person-hours, after which we moved a minimum of 25 m to search another suitable area; sampling areas were not spatially constrained. This was repeated until the sampling period was over. All potential cover objects were searched by hand or with potato rakes, but no single object was searched for more than 20 min. Logs of all sizes in advanced stages of decomposition were pulled apart with potato rakes. Areas beneath large undecomposed logs could not be

Table 1.—Amphibian species captured during time-constrained searches in the southern Washington Cascade Range by stand type.¹

Species	Mean Captures ± Standard Error				
	(N=9) YNG	(N=9) MAT	(N=6) OGW	(N=17) OGM	(N=4) OGD
Caudata					
Plethodontidae					
<i>Ensatina eschscholtzi</i>	5.9±1.8	2.6±0.8	1.2±1.2	2.8±0.9	2.5±1.0
<i>Plethodon vehiculum</i>	3.1±2.2	0.4±0.3	0.2±0.2	0.5±0.3	2.3±2.3
Ambystomatidae					
<i>Ambystoma gracile</i>				0.3±0.1	
<i>A. macrodactylum</i>			0.2±0.2	0.1±0.1	
Salamandridae					
<i>Taricha granulosa</i>				0.1±0.1	0.5±0.5
Dicamptodontidae					
<i>Rhyacotriton olympicus</i>		0.1±0.0		0.1±0.1	
Anura					
Leiopelmatidae					
<i>Ascaphus truei</i>		0.2±0.1		0.2±0.1	
Ranidae					
<i>Rana aurora</i>	0.1±0.1				
<i>R. cascadae</i>				0.1±0.1	

¹YNG=Young, MAT=Mature, OGW=Wet Old Growth, OGM=Moderate Old Growth, OGD=Dry Old Growth

searched in most cases. Little effort was expended searching leaf litter, as this has been shown to be relatively ineffective when sampling amphibians in Douglas-fir forests (Bury and Raphael 1983). Areas near seeps, streams, ponds, rock outcrops, and other areas not representative of the stand were avoided.

Modifications of methods developed by Raphael (1984) were used to describe capture sites. The following information was recorded for each individual captured: species, vertical position in relation to cover object, snag or log decay class, length and width of cover object, and slope and aspect of capture site. All amphibians were collected, measured, and preserved, usually on the same day. Snout-vent length (to anterior margin of vent), total length, and weight were recorded. Specimens were deposited in the Museum of Vertebrate Zoology, University of California, Berkeley.

Results

Captures

A total of 214 amphibians, including 6 species of salamanders and 3 species of frogs, were captured; no reptiles were encountered (table 1). Only two species of plethodontid salamanders, the ensatina (*Ensatina eschscholtzii*) and western redback salamander (*Plethodon vehiculum*), were captured in sufficient numbers (141 and 50, respectively) to permit comparisons of abundance among stand types or to conduct analyses of cover object use.

Habitat Occupancy

Ensatinas and redback salamanders occurred in all forest age and moisture classes. Although both species

were most abundant in young forests (table 1), a one-way ANOVA revealed no significant differences among stand types. Mean captures for both species were lowest in wet old-growth stands. The proportion of stands containing ensatinas was also relatively low in wet old growth: fewer than 20% of wet old-growth stands sampled contained ensatinas, whereas all other stand types had a frequency of occurrence of 65% or greater (fig. 2). The proportion of stands containing redback salamanders was generally low in all stand types (fig. 2), suggesting that at the time of our sampling, redback salamanders were less abundant or more clumped in distribution than ensatinas. We found no amphibians in 67% of old-growth wet stands, 11% of young and mature stands, 12% of moderate old-growth stands, and 0% of dry old-growth stands.

Use of Woody Debris

Cover object selection varied between the two species. Ensatinas

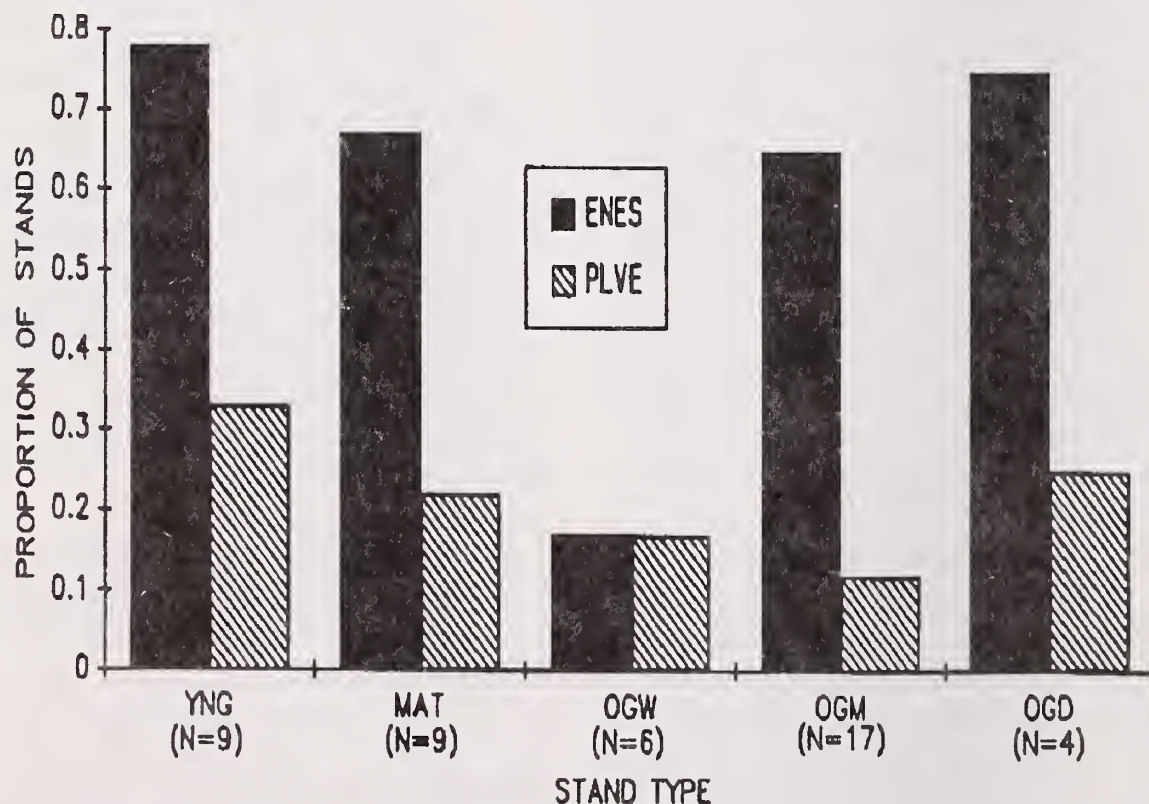


Figure 2.—Proportion of stands in each stand type with captures of *Ensatina eschscholtzii* (ENES) and *Plethodon vehiculum* (PLVE) in the southern Washington Cascades Range. Stand type YNG=Young, MAT=Mature, OGW=Wet Old Growth, OGM=Moderate Old Growth, OGD=Dry Old Growth.

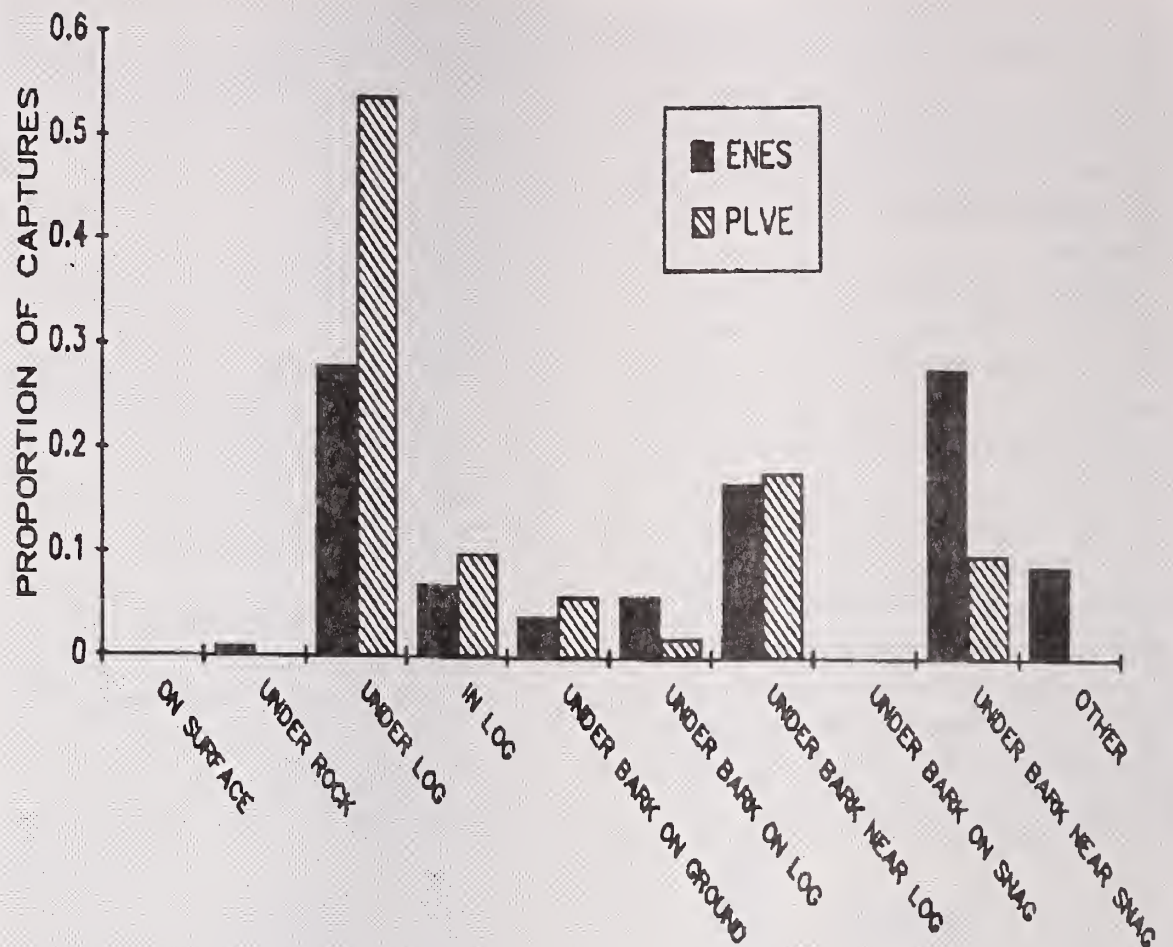


Figure 3.—Use of cover objects by *Ensatina eschscholtzii* (ENES) and *Plethodon vehiculum* (PLVE) in the southern Washington Cascade Range.

were most often found under pieces of bark (generally within 1 m of a snag or log) and secondarily under logs (fig. 3). The pattern was reversed for redback salamanders. Neither species was found under bark on snags. When found under pieces of bark, ensatinas most often occurred in bark piles at the base of moderately decayed snags (see Thomas et al. 1979, p. 64). Seventy-four percent of these captures occurred next to snags in which the top had broken off, the wood was soft, and most or all of the bark had sloughed onto the ground. Logs where ensatinas and redback salamanders were captured were most often 10-30 cm in diameter (fig. 4). Both species were captured in low numbers in association with very large logs (diameter >30 cm), but our inability to adequately search this cover type may account for these results. Virtually all logs where ensatinas and redback

salamanders were found were in intermediate stages of decay (fig. 5) (see Maser et al. 1979, p. 80). Only a few captures of either species occurred in association with intact or extensively decomposed logs. Neither species was commonly found under rocks, but this cover type is relatively rare in Douglas-fir forests. No correlations between slope or aspect and amphibian capture sites could be detected.

Discussion

Old-growth forests do not appear to provide unique habitat for either ensatinas or western redback salamanders; both species were well-represented in all age classes. Our results suggest that abundance levels of these salamanders are more likely a function of the availability of woody debris for cover than age of the overstory. Wet old-growth stands in southern Washington, however, apparently provide low quality habitat for these plethodontids, especially ensatinas (table 1, fig. 2). Soils in these stands were often saturated

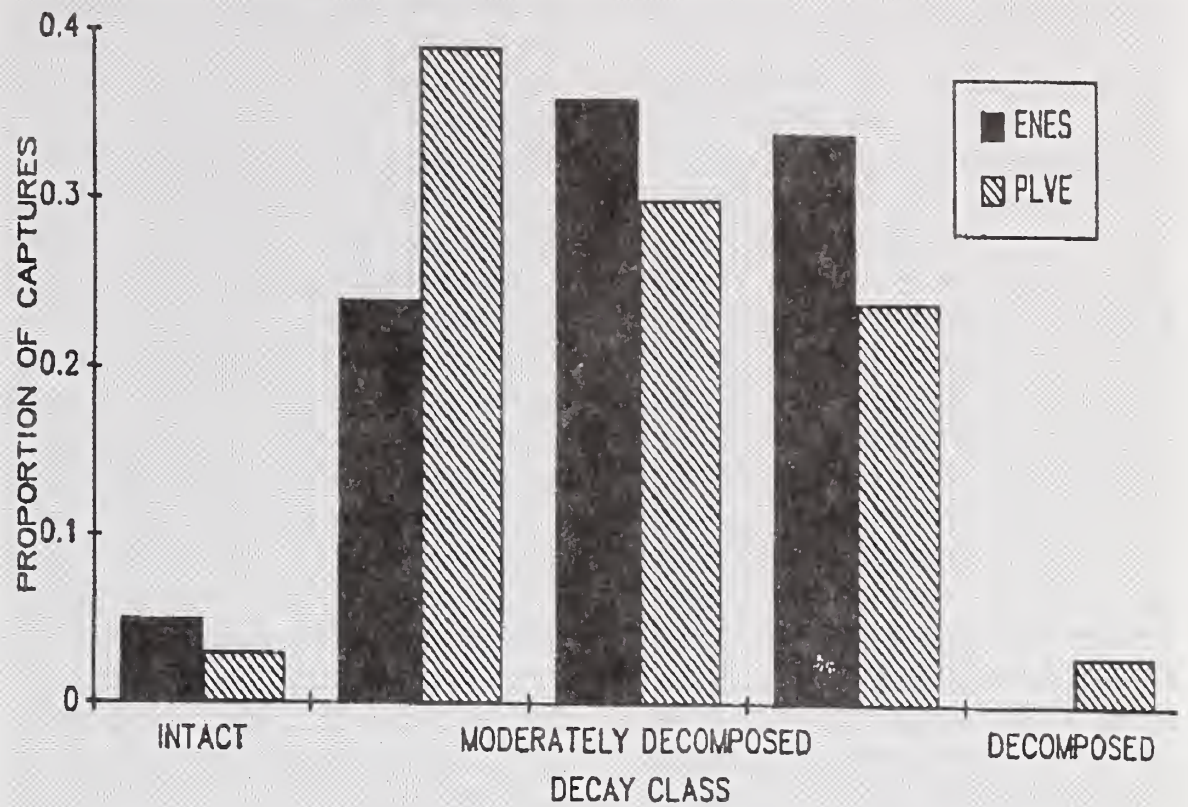


Figure 5.—Use of logs by *Ensatina eschscholtzii* (ENS) and *Plethodon vehiculum* (PLVE) by decay class in the southern Washington Cascade Range.

with water, and such conditions may reduce the availability of microenvironments suitable for cover, maintenance of water balance, and successful reproduction. In addition, these

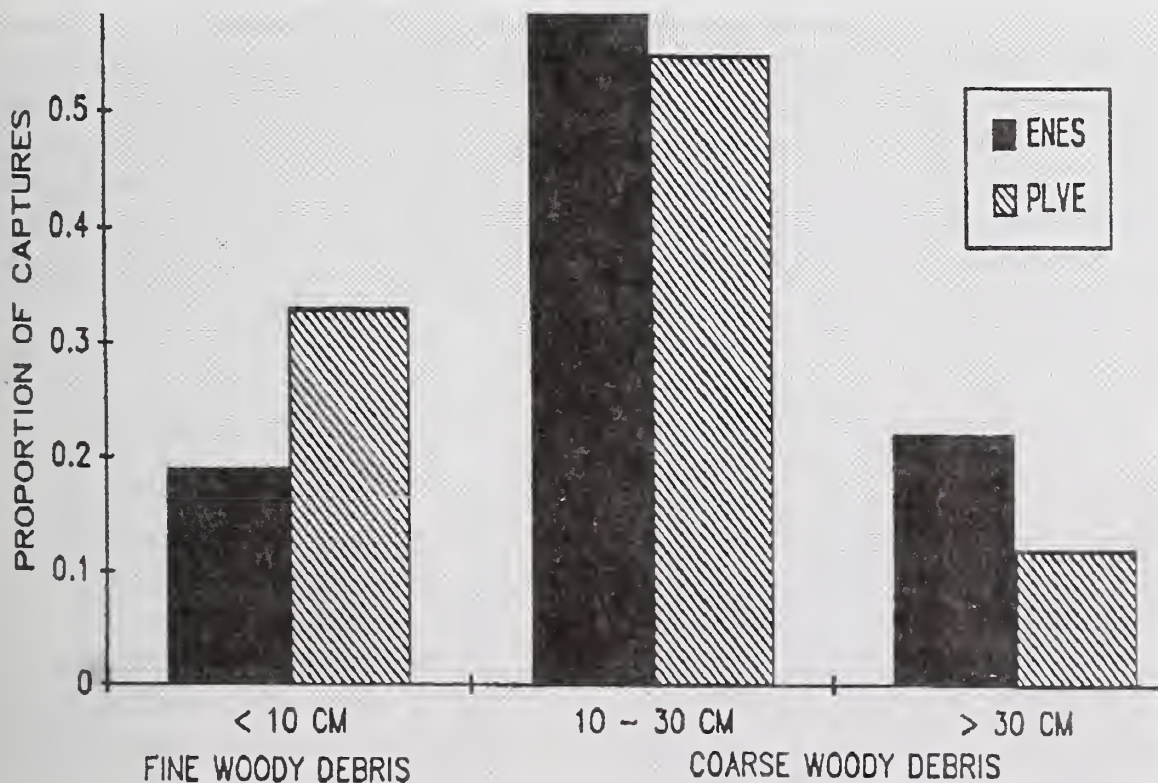


Figure 4.—Use of logs by *Ensatina eschscholtzii* (ENS) and *Plethodon vehiculum* (PLVE) by diameter class in the southern Washington Cascade Range.

stands were located in topographically low sites where cold air accumulates, which may create unfavorable microclimatic conditions for plethodontid salamanders. Our results also suggest that plethodontid salamanders may prefer certain types of woody debris as cover, especially those associated with large, moderately to well-decomposed snags and logs. Captures of ensatinas were most common under pieces of bark, especially in bark piles at the base of well-decayed snags (fig. 3). Snags in the early stages of decomposition with shallow or no bark piles at their bases provide few suitable microhabitats for salamanders. Depth of these bark piles increases as sloughing continues until all bark has fallen off. Later stages of snag decomposition provide no additional bark to the pile and habitable spaces become compressed as the lower layers of bark decay and mix with the underlying substrate.

Bark microhabitats formed by the deterioration of snags differ in structure from those formed by the de-

composition of logs. As logs decay, a single layer of bark is deposited on the forest floor, whereas bark sloughing from snags forms multilayered, structurally complex cover. Such bark piles could provide microclimatic conditions more resistant to fluctuations in temperature and moisture than those found under bark on the ground. Additional foraging habitat may also be available.

Redback salamanders, on the other hand, were most often found under moderately decayed logs 10-30 cm in diameter (figs. 3-5). In the early stages of decay, bark has not begun to slough and branches suspend the log above the ground. As the bark begins to slough and branches deteriorate, increased cover and moisture are provided along the length of the bole where it comes in contact with the forest floor (Maser and Trappe 1984). The quality of this environment for salamanders continues to improve with further decay until the organic matter becomes incorporated into the underlying substrate and habitable interstices become compressed in the advanced stages of decomposition.

All known nest sites of ensatinas in the Pacific Northwest have been found in association with large, moderately decayed logs (Norman and Norman 1980, Maser and Trappe 1984, Jones and Aubry 1985, Norman 1986, L. L. C. Jones unpubl. data). This habitat feature may be important for the persistence of ensatinas in these forests. We do not know to what extent coarse woody debris may be important for reproduction of redback salamanders in Douglas-fir forests; only one nest site has been found, and this was in moist talus in the Oregon Coast Range (Hanlin et al. 1978).

In Douglas-fir stands of the Cascade Range that have regenerated after catastrophic fires, levels of coarse woody debris (CWD) (logs and snags > 10 cm in diameter) are moderate in young stands, lowest in mature stands, and highest in old-

growth stands (Spies et al. *in press*). In general, this is due to the inheritance of high levels of CWD in young stands from the preceding old-growth stands, a low accumulation of CWD in mature stands as CWD decays but inputs are low, and high inputs of CWD in older stands as the large Douglas-firs die and accumulate as snags and logs. Intensive forest management results in levels of CWD substantially lower than that encountered in unmanaged forests (Spies and Cline *in press*). This is because plantations inherit little CWD from the preceding stand when it is clearcut and existing CWD is removed and fragmented. In addition, thinning operations reduce the input of CWD from suppression mortality and short rotations prevent the accumulation of CWD. Maintaining even moderate amounts of CWD in managed forests will require modifications of current harvesting and silvicultural practices (Harmon et al. 1986, Spies et al. *in press*).

Virtually all available cover objects we encountered were woody debris, and both species were found most often in association with large, moderately decayed logs and snags. Our results suggest that the availability of coarse woody debris may be important for maintaining salamander populations in Douglas-fir forests. Additional studies of terrestrial salamanders in managed vs. unmanaged forests are necessary to determine the extent to which they may be affected by intensive forest management.

In general, our study yielded a relatively low number of captures. Only two common species (Nussbaum et al. 1983) were captured in high enough numbers to permit analyses of the data; captures of all other species were incidental. The total number of species detected was also low in relation to known species richness: pitfall trapping for approximately 1000 trap nights in each of the same study sites in the fall of 1984 yielded 916 captures of 13 species (K.

B. Aubry unpubl. data). Research using time-constrained searches to study all but the most common species in this region would require substantially more search time. Sampling should also be conducted during all seasons of the year to detect seasonal shifts in habitat selection or cover object use, and to sample species that are active at other times of the year.

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Forestry Operations and Terrestrial Salamanders: Techniques in a Study of the Cow Knob Salamander, *Plethodon punctatus*¹

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Increasing emphasis is being placed on conservation and preservation of biological diversity worldwide (Norse et al., 1986; Wilson, 1988). U.S. federal and state agencies have become concerned about the biodiversity of their managed lands and are directing efforts towards preserving natural biota. From a management perspective, research on amphibians and reptiles lags behind that devoted to game animals, such as some mammals, birds, and fish (Bury et al., 1980). This is partly due to a previous lack of interest in these groups, but also because some species can be more difficult to observe or investigate.

The Cow Knob salamander, *Plethodon punctatus*, is a dark, moderately large (to 74 mm snout-vent length), woodland, fossorial amphibian (Martof et al., 1982) found only

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on Shenandoah and North Mountain of western Virginia and eastern West Virginia (Highton, 1972; Tobey, 1985). Most of the known range of this recently described species (Highton, 1972) is in the George Washington National Forest. Fraser (1976) compared some aspects of the ecology of this species with a sympatric congener, *Plethodon hoffmani*. Little else is known of the ecology of this salamander. Because of its relatively small range and unknown status, *P. punctatus* was added to the U.S. Fish and Wildlife Service's Category 2 list (U.S. Fish and Wildlife Service, 1985). Potential timber harvesting within the range of this species (USDA Forest Service, 1986) prompted us to examine its status in forest stands of various ages. In this paper we report the following aspects of this study: techniques of capture and data collection, salamander habitat characteristics, and potential effects of logging operations. Our objective in this paper is to make other researchers aware of the techniques we used and the problems we encountered in developing useful management recommendations for the protection of an apparently rare terrestrial salamander.

Materials and Methods

We conducted this study on Shenandoah Mountain, Augusta and Rockingham Counties, George Washing-

Abstract.—The status and ecology of *Plethodon punctatus* was investigated in George Washington National Forest, Virginia to determine potential effects of logging. Pitfall traps and mark-recapture supplemented searching by hand. Elevation, aspect, soil characteristics, and number of cover objects (rocks) are the most important features that identify *P. punctatus* habitat. Intensive logging operations appear to be detrimental to this species.

ton National Forest, Virginia. Before its purchase, between 1911 and 1940, by the U.S. government, this area was repeatedly logged and burned (Leichter, 1987; original land deed documents). Few virgin stands of forest remain, and regrowth and logging operations has resulted in a mosaic of mixed hardwoods of various ages.

We selected five sites of different aged forest to determine the relative abundance of *Plethodon punctatus* (fig. 1) to see if its presence was affected by logging. All sites selected had similar aspects (S-SE) and elevation (914-1127 m) (table 1). We used USDA Forest Service compartment descriptions and maps to aid in selection of sites and to obtain information on the history, physical and biological descriptions, and future management goals for each site. A compartment is divided into a series of stands, each of which defines a forested area of similar tree species by composition, age, and stand condition. Stand age is defined by the age of dominant canopy trees. Final choices of sites were made only after each was checked in the field and tree age was verified by tree ring analysis.

In each site we erected drift fence arrays (Campbell and Christman, 1982) consisting of four 60 cm x 7.5 m sections of aluminum flashing arranged in a cross pattern. Opposite arms of the cross were separated by 15 m and all sections were sunk in

the ground approximately 10 cm. A 5-gal plastic bucket was placed in the center of each arm and #10 cans were placed in the ground on either side of the ends of each arm so that the tops of the pitfalls were flush with the ground surface. Sites A and C contained two drift fence arrays, and the remaining three sites had one array each. In each pitfall we put 4-10 cm of 10% formal-dehyde solution to insure adequate preservation of the salamanders. We selected this method to obtain samples of all the terrestrial fauna for a range of stud-

ies on reproductive cycles and ecology. Pitfalls were checked and all captures (including other vertebrates and all invertebrates) were collected weekly May 5 - June 18, 1987, bi-weekly July 7 - November 22, 1987 and monthly December 1987 and January 1988. Samples were sorted in the laboratory and the vertebrates stored in 10% neutral buffered formaldehyde. Invertebrates were stored in 70% isopropanol.

Hand-collecting supplemented drift fence collection and was used to determine the elevational range of *P.*

punctatus and to obtain information on range and habitat characteristics. Results from timed collecting periods allowed comparison among sites and dates of collection. Between April 20 and June 2, 1987, we collected data on eleven microhabitat variables at 67 sites to evaluate those most important in predicting the presence of this salamander. These variables were elevation, aspect, slope, soil temperature under cover object, soil moisture, soil pH, soil description, canopy cover, number of cover objects available within a 2 m circle, type of cover object (e.g., rock, log), and forest type.

One site >1 km away from any of the collection sites was selected for estimation of population size and data on individual movements. We searched for salamanders in daylight by turning and replacing all surface objects and at night while they were active on the surface (i.e., during conditions of near 100% relative humidity [sensu Heatwole, 1960; Jaeger 1978]). Each individual was measured (snout-vent length, tail length to nearest mm), weighed (nearest 0.1 g), the sex determined, assigned to adult or juvenile age-classes, marked by toe-clipping, and released at its capture site. We marked each capture site with survey flags on which the salamander's number and capture



Figure 1.—*Plethodon punctatus*, the Cow Knob salamander, from Shenandoah Mountain, Augusta County, Virginia. Photograph by Kurt A. Buhlmann.

Table 1.—Descriptions of drift fence study sites for *Plethodon punctatus* on Shenandoah Mountain, Virginia. Slope angle is in degrees and site age is in years since last logging activity.

Site	Timber descrip.	Slope	Manag. type	Site age	Stand condition	Past logging history
A	1 yr old white pine several hardwood seed trees	30	white pine	2	seedling/ sapling	90% clearcut few hardwood trees
B	white oak/ red oak/hickory	45	oak/hickory	8	sparse saw timber	thinned due to ice damage, 1979
C	white pine/mixed hardwoods	25	white pine	30	immature pole timber	cut in 1956, planted in white pine, some hardwood seed trees
D	white oak/hickory	30	oak/hickory	60-100	mature saw timber	no recent management
E	white oak/ red oak/ hickory	5	none	virgin?	low quality saw timber	none known

date were written. We noted all recaptures and measured movements in linear fashion (0.1 m) between capture points.

Results and Discussion

Capture Techniques

Nineteen *P. punctatus* were caught in the pitfall traps, 2.0% of the total number of salamanders. Of the 17 recorded, 12 were caught in 5-gal. buckets and 5 in #10 cans. Eleven *P. punctatus* were caught in Site E, six in Site B, and two Site D. None were caught in Site A or the Site C. In contrast, by hand collecting in areas adjacent to Site E, we found 38 *P. punctatus* in 7.7 man hours of searching. The drift fence method appears only moderately effective in sampling this salamander. It is feasible that *P. punctatus* is less likely to fall into the pitfalls than other salamander species. We observed several individuals climbing rocks and tree trunks during nocturnal surface activity. This suggests that this salamander is able to detect precipices and avoid falling into pitfalls. Also, this species may be active on the horizontal surface only for limited periods of time and under specific environmental conditions. Thus, the drift fence technique, which depends on horizontal activity, may not be an effective sampling method for this salamander (R.D. Semlitsch, pers. comm.).

Data from pitfall traps, combined with data from hand collecting, can provide information for management decisions. For instance, seasonal trends in surface activity were similarly indicated by both drift fence results (fig. 2) and captures based on hand collection (fig. 3). Comparison of *P. punctatus* with that of its sympatric congener *P. cinereus* (fig. 3) reveals concordance in seasonal activity and suggests similar responses to surface environmental conditions. This information could be used to determine the times logging opera-

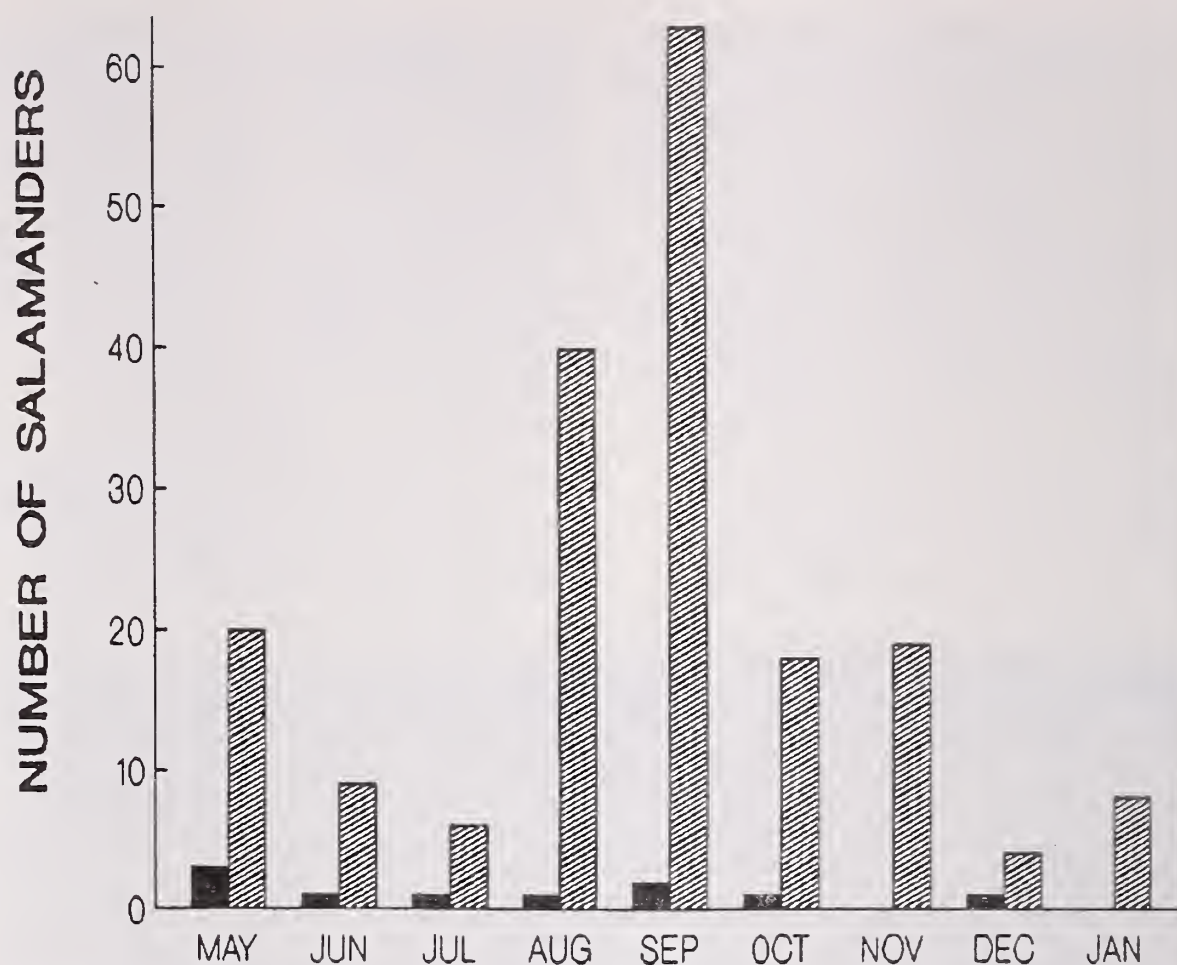


Figure 2.—Seasonality of drift fence captures of *Plethodon cinereus* and *P. punctatus* at Site E (Tomahawk Mountain), George Washington National Forest. Adults and juveniles are included, but not hatchlings. Sampling period is 5 May 1987 to 24 January 1988.

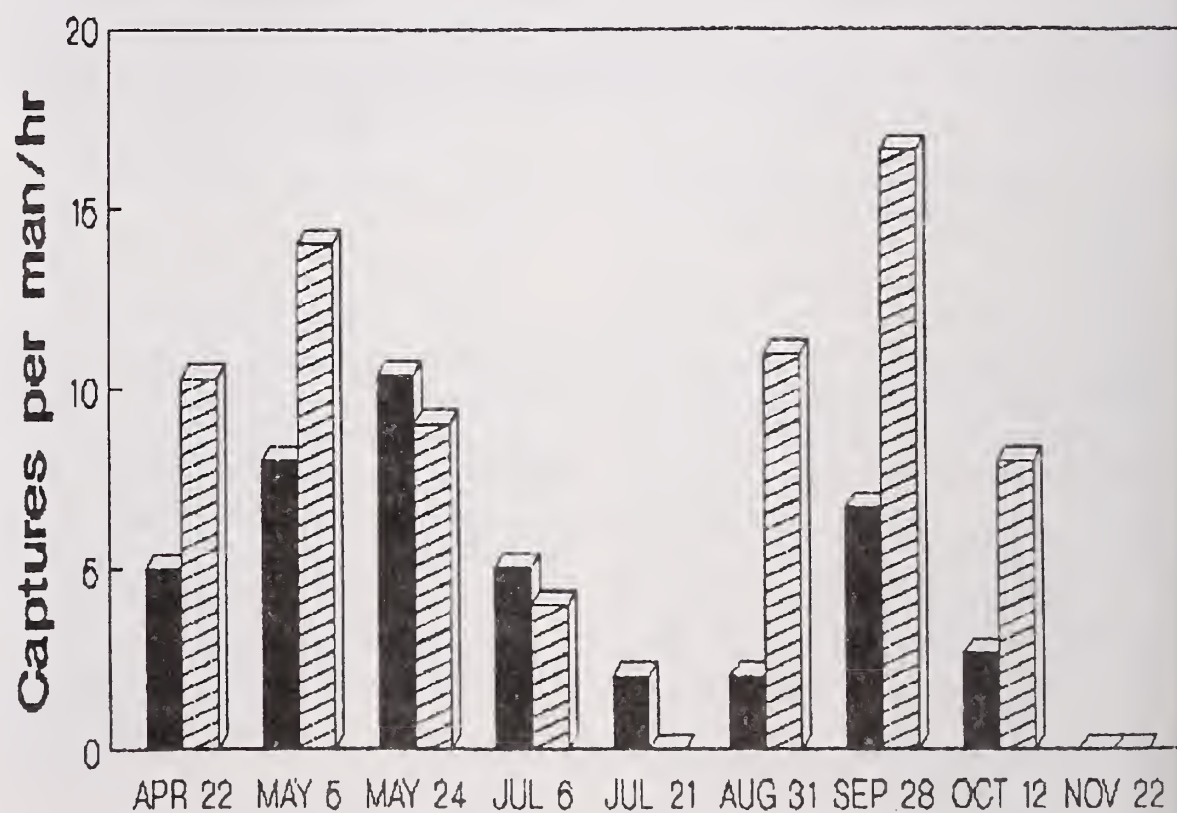


Figure 3.—Seasonality of captures per man hour of *Plethodon cinereus* and *P. punctatus* on Tomahawk Mountain, George Washington National Forest. Black bars represent *P. punctatus* and bars with diagonal lines represent *P. cinereus*. Sampling dates are 22 April to 22 November 1987.

tions would cause the least impact on salamanders at or near the surface.

The benefits of the drift fence technique outweighed the low numbers of captures of *P. punctatus*. We probably would not have otherwise found this species in Site D because there were few surface rocks to turn over. Although the individuals caught may have been transients, this species does occasionally occur at this site. This result would not have been obtained by hand-collecting alone.

The drift fence method also provided estimates of the relative abundance of the salamander fauna and other species in the community. The relative numbers of these species and species groups can generate additional information on the structure of the community in which the focal species lives. Drift fence techniques have been used for a variety of ecological studies (e.g., Gibbons, 1970; Gill, 1978; Pechmann and Semlitsch, 1986) but only recently to answer questions about vertebrate communities in relation to forest management (e.g., Bennett et al., 1980; Gibbons and Semlitsch, 1981; Enge and Mar-

ion, 1986; Bury and Corn, 1987). Our results indicate this technique can be effective in mountainous terrain and can be used to gain information on apparently rare terrestrial salamanders.

If an endangered or otherwise protected species is the focus of study and cannot be collected, then slight modifications of the drift fence-pitfall design must be made. Traps would need to be checked on a daily basis, or nearly so, in order to release the animals unharmed (Gibbons and Semlitsch, 1981). Water or wet leaves can be placed in the pitfalls for cover and moisture. Potential problems include killing of the salamanders in the pitfalls by small mammals, especially shrews, and desiccation. The loss of animals by shrew or raccoon predation in pitfall containers affects the samples and may prevent quantitative comparisons among sites. Data obtained from visitation frequencies of every three days (Bury and Corn, 1987) to once a week (Enge and Marion, 1986) probably underestimate actual captures.

The detection of *P. punctatus* at a particular site depends on the time of year, substrate type, soil depth, soil moisture, soil temperature, and weather conditions (see Habitat Requirements). A simple survey of sites by hand searching and rock turning in daylight hours without attention to weather and seasonality will underestimate actual abundance and fail to detect presence of a species. Table 2 contains comparative data for two sites searched the same day at different times of the year and demonstrates a strong seasonal effect. In order to construct effective management plans, the range and abundance of a terrestrial salamander must be known. Therefore, researchers conducting distributional surveys must take seasonal and diel changes in surface activity into consideration.

Results of our 1987 mark-recapture efforts are preliminary; only

four recaptures were made. One *P. punctatus* captured 28 May was recaptured on 15 October. It had moved 17.4 m. Three salamanders were recaptured within ten days of original capture and had moved ≤ 2 m. Knowledge of movement capabilities by *P. punctatus* is an important part of evaluating the consequences of population fragmentation through logging operations. Are salamanders able to move out of a logged area or repopulate it when suitable habitat conditions return? We believe mark-recapture studies can provide useful information on rare terrestrial salamanders, but realize that data may need to be collected over several years and under standardized conditions in order to provide direct answers.

Habitat Characteristics

Preliminary evaluation of microhabitat data indicate that four site characteristics are most important in determining the presence of *P. punctatus*. We found *P. punctatus* at elevations between 732 m and 1317 m (fig. 4). Most sites (87%) with this species occurred above 960 m. *Plethodon punctatus* occurred on all slopes but were more common on north-facing aspects (87% of 11 sites) than east (38% of 13), south (36% of 8), or west aspects (40% of 7). Most of the captures (67% of 21) were on slopes of 20-45°. Seven sites were on slopes less than 20° and between 46° and 60°. Sites without this salamander were on a similar range of slopes (< 20°, 28.6%; 20-45°, 57.1%; > 45°, 14.3%).

Soil temperatures under cover objects at sites with *P. punctatus* ($x = 12.3$ C, 9.4-16.1, $n = 36$) were nearly identical to temperatures at sites without this species ($x = 12.8$ C, 9.4-15.8, $n = 15$). Soil pH under cover objects were also similar (with *P. punctatus*: $x = 6.3$, 5.4-6.8; without *P. punctatus*: $x = 6.4$, 5.8-6.8). Average soil moisture at sites with *P. punctatus* was 37.1% (12- 70%) and 42.8% (24-

Table 2.—Seasonal differences in surface abundance of *Plethodon punctatus* at Flagpole Knob and Skidmore Tract, Shenandoah Mountain, George Washington Forest. These sites are <1 km apart. Flagpole Knob is a rocky, grassy ridge habitat containing young oak (*Quercus* sp.) and maple (*Acer* sp.) pole timber, and Skidmore is a virgin hemlock (*Tsuga canadensis*)/yellow birch (*Betula lutea*) forest. Numbers of salamanders are followed by number of man hours in parentheses. All data are based on hand-collecting results.

Date	Flagpole	Skidmore
June 2	11 (0.5)	10 (1.7)
June 8	0 (0.5)	2 (2.0)
Sept. 28	0 (1.0)	3 (3.0)

80%) at sites without this species. Soils in which *P. punctatus* were found are characterized by shallow black humus intermixed with rocks (72% of 39 sites). One site where eleven salamanders were captured consisted of brown humus and extensive log cover, but few rocks. Cover objects under which this salamander was found were rocks < 645 cm² (13.6%), rocks 645-1290 cm² (40.0%), rocks > 1290 cm² (34.8%), and logs (10.6%). Over 89% of the captures were found under rock cover. Number of cover objects within a 2 m circle of the captured salamander averaged 15.1 (1-45). Sites without *P. punctatus* ranged from 100% rock cover to 0% rock cover. Sites with canopy cover equal to or greater than 50% accounted for 88.2% of the captures (n = 52).

We found *P. punctatus* in the following forest types: mature oak/hickory (38.5% of 13), oak/maple/birch (62.5% of 8), oak/pine (33.3% of 3), young oak/maple/hemlock (50% of 8), virgin hemlock/yellow birch (100% of 2), hemlock/maple/basswood (62.5% of 8), white pine (0% of 2), and grassy balds (20% of 5). Of the site characteristics we examined, the following appear to be most important in identifying *P. punctatus* habitat: elevation, aspect, soil characteristics, and number of cover objects (rocks).

Habitats of terrestrial salamanders differ among species and, in some cases, among geographic areas within species (e.g., Semlitsch, 1980; Tilley, 1973). Data derived from the literature for management studies and plans must be used with caution. Baseline habitat and life history studies should be conducted on the focal species at the location in question before developing management plans.

Effects of Logging

Tree removal effects the terrestrial salamander community in several ways. Removal of canopy cover

eliminates the moisture-retaining potential of the soil and leaf litter, allows an increase in insolation (with a concomitant increase in soil temperatures), and increases soil erosion (Bury, 1983).

The use of heavy machinery compacts soil and destroys leaf litter. Enge and Marion (1986) found that machine site preparation and clearcutting had little effect on amphibian species richness in a Florida slash pine forest. However, of the 15 amphibian species they recorded, none was a terrestrial salamander. On Shenandoah Mountain, where most of the terrestrial amphibian community is comprised of terrestrial salamanders, logging and clearcutting are likely to have detrimental effects. Salamander abundance in a 60-100 yr-old deciduous forest in another Virginia site was more than four times that in 2 yr-old and 6-7 yr-old clearcuts (Blymer and McGinnes, 1977). Bury (1983) found that terrestrial salamanders were more abundant in old growth compared to logged redwood forest

habitats. *Plethodon cinereus* was significantly less abundant in a clearcut site compared to an old-growth site in a deciduous forest in New York (Pough et al., 1987).

Populations of *Plethodon punctatus* inhabiting rocky substrates with a thin soil cover may be able to withstand some logging operations. Our Site B was logged in a salvage operation after ice storm damage. Not all trees were removed and the substrate was not as damaged as that in Site A, which was clearcut. These factors, combined with the presence of a seep near the drift fence array, probably explain the high numbers of *P. punctatus* found at Site B compared to other logged sites.

We found no *P. punctatus* on Sites A and C for apparently different reasons. Site A was clearcut, the substrate was greatly disturbed, and the lack of canopy cover prevented moisture retention. The fact that *P. punctatus* occurred on the same ridge in a nearby hardwood stand suggests this salamander may have occurred on Site A prior to logging. Site C was

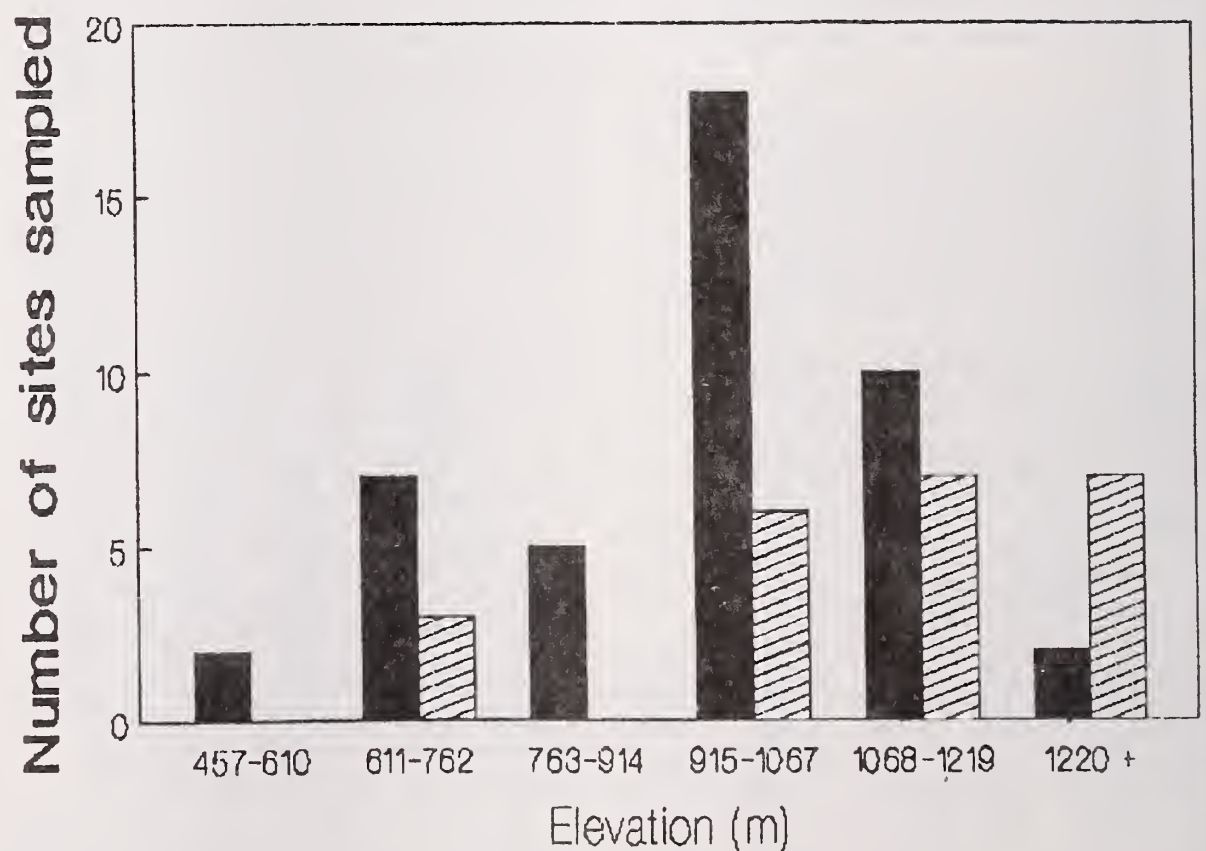


Figure 4.—Elevational distribution of *Plethodon punctatus* on Shenandoah Mountain, George Washington National Forest. Solid bars represent sites where *P. punctatus* was not found and bars with diagonal lines represent sites where this species was found.

logged 30 years ago but was replanted with white pine (table 1). The logging operation and change in vegetation type may have affected the salamander populations previously present. However, because of the lack of rocky substrate, we cannot disprove the hypothesis that *P. punctatus* may not have occurred there historically.

Plethodon punctatus appears to occur in greatest abundance on rocky sites that contain virgin hardwoods (Site E) and sites that are not heavily disturbed by logging operations (Site B). Clearcutting and associated disturbance does appear to eliminate populations of this salamander. Salamander mortality can be minimized if logging operations are conducted outside the seasonal activity period. If size of the area logged is small, or if the area is logged in a mosaic, or if corridors are allowed to remain, reinvasion may eventually be possible from peripheral populations when suitable conditions return. Fragmentation of the limited range of *P. punctatus* by a patchwork of clearcuts could seriously affect its long-term survival.

Conclusions

Because of budget and time constraints, our study attempted to obtain baseline data and evaluate the effects of logging simultaneously. We offer the following conclusions to researchers and managers who must study a salamander whose ecology is little known.

1. Multiple capture techniques should be used when studying an apparently rare terrestrial salamander.
2. The life history and basic ecology of the study species needs to be understood before the project's experimental design can be erected to evaluate logging effects.

3. Seasonal and daily activity patterns of salamander activity must be taken into consideration when surveys are conducted to determine range and population abundance.
4. Project proposals to federal and state agencies should contain a two step process, a field survey phase to obtain baseline data on ecology and life history and an experimental phase in which logging or other concerns are evaluated. The design of the experimental phase should be based on the results of the field survey.

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Conserving Genetically Distinctive Populations: The Case of the Huachuca Tiger Salamander (*Ambystoma tigrinum stebbinsi* Lowe)¹

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Technological advances in genetics now enable characterization of variation within a species at increasingly finer levels of description. These developments are allowing us to begin the difficult task of identifying which gene pools should be protected to preserve genetic attributes significant for conserving present and future generations of a species (Echelle 1988, Meffe and Vrijenhoek 1988, Ryman and Utter 1987). Rather than considering simply which species to conserve, we can now ask whether a conservation effort should be directed at the species, subspecies, or population levels (Allendorf and Leary 1988, Behnke 1972, Ryder 1986).

Tiger salamanders, *Ambystoma tigrinum* Green, range throughout much of North America from southern Canada to the central Mexican Plateau, and from the east coast of the United States to California (Gehlbach 1967). This complex species is divided into eight subspecies (Collins et al. 1980, Gehlbach 1967,

Jones et al. 1988), several of which (*tigrinum*, *mavortium*, *nebulosum*, and *melanostictum*) are widespread geographically, locally abundant, and apparently not in need of protection at this time. More information is needed on the Mexican subspecies, *velasci*, and a north-central USA race, *diaboli*, before conservation needs can be confidently assessed. Two races need consideration now.

A. t. californiense occurs only in the Central Valley and adjacent oak woodlands of California, placing it among the more geographically restricted tiger salamanders. Further, *A. t. californiense* appears to have been isolated from the other races of *A. tigrinum* for several million years, and has a level of genetic divergence equalling species-level differences among many ambystomatid taxa (Jones 1988). Two factors suggest this taxon warrants special conservation efforts. First, California populations are as distinct genetically from other races of tiger salamanders, as other species of *Ambystoma* are from each other. Second, the geographic isolation and apparent spatial subdivision of *A. t. californiense* populations (Gehlbach 1967) likely increases their probability of extinction (Soule 1987).

A. t. stebbinsi has properties like *A. t. californiense*, suggesting it too needs special conservation efforts despite being classified as only part of a very wide-ranging species. Populations of *A. t. stebbinsi* occur only in the San

Abstract.—Huachuca tiger salamanders are a genetically distinctive race of *Ambystoma tigrinum* found only in 17 localities in the San Rafael Valley (SRV) in southeastern AZ. Populations of SRV salamanders are threatened by introduction of exotic fishes and disease. Salamanders were largely eliminated from four habitats after introduction of sunfish and/or catfish. An unknown fatal disease killed all aquatic morphs in two other habitats. An additional threat includes possible hybridization and introgression of SRV populations resulting from introduction of exotic salamanders. Introduced bullfrogs may also prey on salamanders, or act as vectors for disease.

Rafael Valley (SRV) in the borderlands between Arizona and Sonora, Mexico. In addition to being geographically restricted, the race is also genetically distinctive. Average heterozygosity among SRV populations is the lowest in *Ambystoma* (Jones et al. 1988). Electrophoretic analysis, as well as variation in external morphology, indicates *A. t. stebbinsi* is phylogenetically most closely related to *A. t. mavortium*. In contrast, analysis of the mitochondrial DNA (mtDNA) in these populations indicates there is a single mitochondrial clone in the San Rafael Valley. This clone is derived from *A. t. nebulosum*, not *A. t. mavortium*, suggesting *A. t. stebbinsi* actually arose from hybridization between *A. t. nebulosum* and *A. t. mavortium* (Collins 1988).

A recent paper describes patterns of variation in external morphology, allozymes, and geographic isolation that suggest *A. t. stebbinsi* is a distinctive race within the *A. tigrinum* complex (Jones et al. 1988). In a future paper we will describe mitochondrial DNA variation in these populations (Collins et al., in prep.). Our present goal is to summarize several aspects of the population biology of *A. t. stebbinsi*. In addition to being restricted geographically, our research indicates salamander populations in SRV are threatened by several factors including disease, and factors surrounding the introduction of exotic fishes and salamanders.

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Materials and Methods

SRV is a Plains grassland-Madreaan evergreen woodland habitat extending from southeastern AZ into northeastern Sonora (Brown 1982). A survey of aquatic habitats in southern AZ and northern Sonora and Chihuahua indicated salamanders referable to *A. t. stebbinsi* occurred only in SRV (Jones et al. 1988).

From June 1979 to February 1988, we sampled seven natural and 23 man-made or man-altered aquatic habitats in SRV and adjacent slopes of the Patagonia and Huachuca mountains. Altered habitats were primarily livestock watering tanks constructed where natural water formerly existed. Bog Hole tank is a large, impounded cienega (sensu Hendrickson and Minckley 1985), and another may be an impounded spring. Salamanders occurred in only 17 of the 30 habitats sampled in SRV (appendix 1, fig. 1). We report life history variation in *A. t. stebbinsi*, and the influence of disease and introduced exotic animals on this taxon. For describing life history variation we emphasize four tanks (Parker Canyon #1, Huachuca, Upper 13, and Bodie Canyon) sampled routinely. We also present additional information from irregular collections at all other SRV tanks with salamanders.

We usually collected specimens using seines and dipnets, but occasionally used gill nets. Depending on our plans for using a particular collection, we either marked and released salamanders, returned them to the laboratory alive, or preserved them in the field for later analysis. All preserved specimens are in the Lower Vertebrate Collections at Arizona State University.

To summarize life history variation in *A. t. stebbinsi*, we classified salamanders by life history stage and morphology using internal and external characters (table 1). Stages 1 or 2 were immature, and 3-5 were mature. Metamorphosed salamanders lack gills and a caudal fin, while lar-

vae and mature branchiate salamanders have those structures. All measurements are in mm; snout-vent length (SVL) is the distance from snout to posterior margin of the vent.

Results

Life History Variation

Ambystoma tigrinum has the most complicated pattern of morphological and life history variation known in salamanders. After an egg hatches a larva begins growing in an aquatic habitat. At about 30 mm SVL, larvae of *A. t. nebulosum*, *A. t. mavortium*, or *A. t. tigrinum* can continue development as a typical larva, or develop as a cannibalistic larval morph. This dimorphism is unknown in the other subspecies (Collins et al. 1980). At about 70 mm SVL, larvae of all sub-

species except *A. t. californiense* continue developing in one of two ways. They may metamorphose, often leave the aquatic habitat, and must eventually return to freshwater to breed. Alternatively, a larva continues growing beyond 70 mm SVL, matures, and breeds as a larval-like form, or paedomorph (Gould 1977). Thus, depending on the subspecies, a single population might have two juvenile morphs, typical or cannibal, and four adult morphs, typical and cannibal, mature, branchiate morphs or metamorphosed morphs of either type. Relative frequency of each morph varies among populations in a subspecies (Collins 1981, Rose and Armentrout 1976).

In SRV, most populations have mature, typical, branchiate morphs as well as mature, typical, metamorphosed morphs. Judy Tank is one population in which we have col-

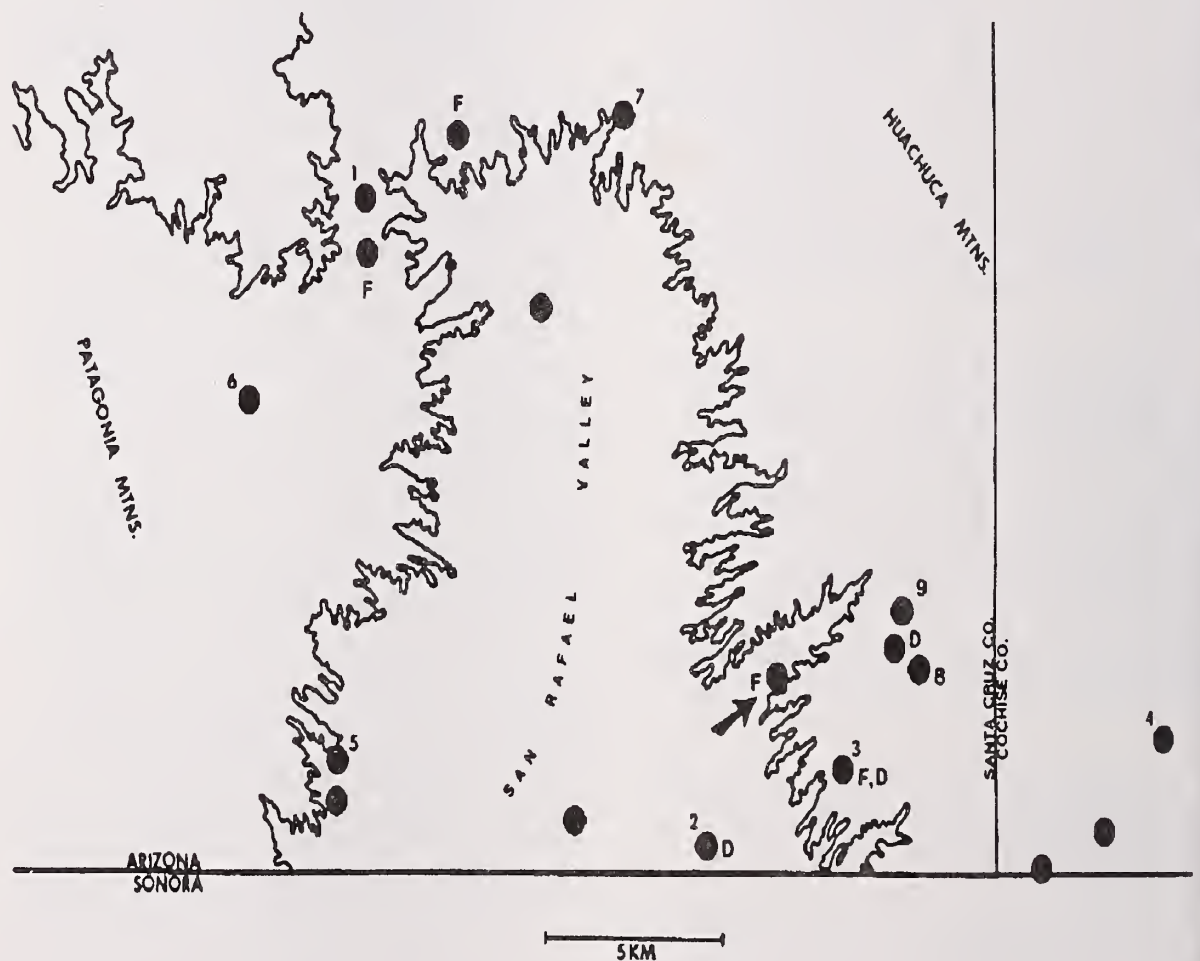


Figure 1.—Map of the San Rafael Valley, Arizona. Symbols indicate sampling sites (see appendix 1). Electrophoretic samples were from sites 1-8; mtDNA samples were from sites 1, 2, 5, 6, 9; F=sites with fish; D=sites with diseased salamanders; arrow=J.F. Jones Ranch, type locality for *stebbinsi*.

lected no mature, branchiate morphs thus far. Mature, typical, branchiate morphs dominated the SRV populations. From July 1979 to August 1985, we collected more than 1200 mature, branchiate salamanders and only 64 mature, metamorphosed animals. We conservatively estimated population sizes of mature, branchiate morphs as varying from 50 (Upper 13 Reservoir, 1984) to several hundred (Huachuca Tank, 1983, 1984). No population in the SRV had cannibalistic morphs. Absence of the cannibal morph is a distinctive feature of these populations, since the morph can be common in *A. t. nebulosum* and *A. t. mavortium*, the nearest relatives of *A. t. stebbinsi*.

losum and *A. t. mavortium*, the nearest relatives of *A. t. stebbinsi*.

Salamanders in SRV bred as early as mid-February and as late as early May. Most egg laying occurred from mid-March to late April. Animals hatched within several weeks and grew rapidly, so that larvae <40 mm SVL were often abundant by late spring (tables 2-5). By mid-July, larvae were usually about 60 mm SVL, and those that metamorphosed generally did so from late July to early September. A relatively small percentage of larvae metamorphose annually—about 17% to 40% based on estimates from Bodie Canyon Tank.

By early autumn, first year animals that did not metamorphose began to mature (tables 2-5). From late autumn through winter most SRV branchiate salamanders were >100 mm SVL (tables 2-5), and ready to breed (figs. 2-3). These data indicate branchiate salamanders in SRV breed for the first time when one year old.

Disease

During July and August 1985, all branchiate salamanders in Inez, Huachuca, and Parker Canyon #1 Tanks were killed by an undiagnosed disease (fig 1). Salamanders in the field and laboratory showed little resistance to the disease which was 100% fatal within a few days of the appearance of symptoms. Attempts to culture the pathogen(s) were inconclusive, but many symptoms resembled those characteristic of *Aeromonas* infection [red leg] (Fowler 1978), including lethargy, loss of appetite, and the epidermis can become red from infusion of blood. This type of epidemic disease in the aquatic environment is particularly devastating in *A. t. stebbinsi*, because population structure in SRV is strongly skewed toward larvae and mature branchiate animals. In addition to death of larvae, therefore, most adults may have been killed in highly infected populations.

Parker Canyon #1 and Inez were recolonized by metamorphosed salamanders that presumably escaped the disease while in terrestrial sites. We collected two metamorphosed adults (male and female) and one larva in Inez Tank in April 1986 and collected eggs in April 1987. We also collected eggs in Parker Canyon #1 in April 1987, and five mature branchiate morphs (3 males, 2 females) in January 1988. Since all branchiate morphs in Parker Canyon were killed in 1985, and none was collected in 1986, these five animals also supported our conclusion that in SRV branchiate salamanders can reach

Table 1.—Criteria used to classify salamanders into stages of breeding readiness. Numerals in parentheses refer to diameter in mm (after Collins 1981).

Oviduct, ovary, peritoneum, and cloacal characters	Wolffian duct, testes, peritoneum, and cloacal characters
1. Gonadal tissue primarily white and flacid; Wolffian ducts or oviducts narrow, with few folds; cloacal margins not swollen; peritoneum largely unpigmented.	
2. Oviducts enlarged (0.5-1), white, weakly convoluted; ova small (<1), mostly white-cream colored; dorsal third of peritoneum light grey; cloacal margins not swollen.	2. Duct enlarged (0.5-1), convoluted, but not distended in coils; testes small, flacid; peritoneum black; cloacal margins swollen, with grey to grey-black borders, especially posterior.
3. Oviducts large (3-4), convoluted, white; ova small and white, medium (1- 1.5) and cream or cream-tan or black, with some perhaps large (1.5-2) and bipolar cream and tan; at least dorsal two-thirds of peritoneum grey to black; cloacal margins swollen, bulbous with interior margins light grey to black and rugose.	3. Duct large(>1), convoluted, cream colored with localized black pigment; testes turgid; cloacal margins swollen, grey to grey-black, rugose borders, especially posterior; peritoneum black, especially densely pigmented dorsally.
4. Oviducts large, convoluted, white, distended in coils; ova small and white or large and bipolar cream and tan; peritoneum and cloaca as in 3.	4. Duct large, convoluted, cream colored with scattered black pigment spots, distended in coils; testes turgid, enlarged; cloaca and peritoneum as in 3.
5. All characters as in 3 except most ova small and white with a few darkly pigmented.	

sexual maturity when a year old. We collected no salamanders in Huachuca Tank as late as spring 1988 (see below).

Introduction of Exotic Animals

Fishes.—A few exceptional species of salamanders can coexist with fishes, but most cannot. In SRV exotic fishes, especially centrarchids and ictalurids, invariably eliminate salamanders. We do not know the effect of native fish on *A. t. stebbinsi*, but no salamanders occur in four natural SRV habitats (Heron Spring, Sheehy Spring, Sharp Spring, Santa Cruz River and tributaries) that have native fishes (*Gila topminnow*, *Poeciliopsis o. occidentalis* and *Gila chub*, *Gila intermedia*). We base our general conclusions concerning exotic fishes and salamanders in SRV on the following observations (fig.1).

J.F. Jones Ranch Tank.—This is the type locality for *A. t. stebbinsi*. Largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) were introduced in the 1950s, and salamanders no longer occur here (see photograph of this site in Lowe 1964:106). It is apparently a popular local fishing spot.

FS 58 Tank.—We first collected mature, branchiate and larval salamanders here in July 1979. There were only yellow bullheads (*Ameiurus natalis*) in June 1980. In August 1984, we collected 19 mature, branchiate salamanders, no catfish, and hundreds of sunfish (*Lepomis* sp.).

Huachuca Tank.—First sampled in May 1982, this tank was a reliable source of salamanders and natural-history information for the next two years. On 22 August 1984 we found one yellow bullhead, plus many larval and mature branchiate salamanders. On 5 July 1985 we netted >100 salamanders in each of several seine hauls. Routine sampling on 24 August 1985 yielded several thousand fingerling catfish and no salaman-

Table 2.—Seasonal variation in number and size (SVL) of salamanders in each breeding stage collected from Parker Canyon Tank.

Date	Stage	Snout/Vent Length (mm)					
		0-19	20-39	40-59	60-79	80-89	100-119 120-140
8 Jan	4						5
28-29 Mar	1	13					
	4						7 2
22-28 Apr	1	4	6				
	4						39 8
	5						4
13-25 Jun	1		3	36			
	2						1
	3					6	9 1
	4					1	19 10
	5					4	4 14
5-10 Jul	1		1	18			
	4						7 1
	5						1
22 Aug	1				7		
	2					2	
	3						7 3
	4						9 1
2 Dec	4						10 18

Table 3.—Seasonal variation in number and size (SVL) of salamanders in each breeding stage collected from Upper 13 Reservoir.

Date	Stage	Snout/Vent Length (mm)					
		0-19	20-39	40-59	60-79	80-89	100-119 120-140
8 Jan	4						2
17 Mar	4						5
7 May	1	11	43				
24 Jun-	1		20	79	24	8	
9 Jul	2					13	
	4					1	7
	5					2	5 1
23-28 Aug	1					1	
	2						1
	3					4	11
	4						3
9 Oct	1				2		
	2				4	2	
	3				1	1	2
	4						4
10 Nov	1				1	2	
	3					1	
2 Dec	4						5

ders. We resampled this site several times through February 1988. Each time we caught only catfish, although salamanders were abundant in nearby tanks.

In this instance disease as well as predation may have contributed to decline of the salamander population. On 24 August 1985 we found

three dead mature, branchiate morphs in the tank. We also observed a significant decline in salamander populations on this date at two other tanks with diseased salamanders. Yellow bullheads are highly carnivorous (Minckley 1973), and we do not expect salamanders to successfully recruit at Huachuca

Tank as long as the catfish population remains high. Catfish will presumably eat eggs, larvae, and all but the largest salamanders. We know of no experiments demonstrating the minimum number of catfish that will prohibit salamander reproduction.

Bog Hole Tank.—We collected salamanders here in 1979, 1980, and one larva in 1982. Native fishes comprised longfin dace (*Agosia chrysogaster*) and Gila topminnow. Since the 1970s, several exotic fishes including *Gambusia affinis*, *Cyprinodon macularius eremus*, *Lepomis* spp., and *Micropterus salmoides* (W.L. Minckley, pers. comm.; Minckley and Brooks 1985) have become established. Disappearance of *A. t. stebbinsi*, and the two native fish species, correlates with establishment of non-native fish populations.

Frogs.—During the last decade bullfrogs (*Rana catesbeiana*) were introduced in SRV. Their introduction correlates with reduction in native frog populations in the valley, but the impact of bullfrogs on *A. t. stebbinsi* is unknown. Bullfrog larvae may eat salamander eggs, while adults may prey on larval salamanders. Bullfrogs may also act as vectors for disease, since in the three tanks where salamanders were heavily affected by disease, bullfrog populations were large and apparently unaffected. Frogs may be a natural reservoir for disease, and suffer few negative effects from the pathogen(s). Since they disperse readily to colonize surrounding habitats, they may also help spread disease among amphibian populations.

Salamanders.—Commercial baitdealers (waterdoggers), fishermen, and private landowners introduce native and exotic salamanders into aquatic habitats in Arizona (Collins 1981). Salamanders are used commonly as bait by fishermen in the American Southwest (table 6), and Lowe (1955) first noted that salamanders were being introduced into Arizona for this purpose. SRV is closed to "waterdog" collecting under Ari-

Table 4.—Seasonal variation in number and size (SVL) of salamanders in each breeding stage collected from Huachuca Tank.

Date	Stage	Snout/Vent Length (mm)					
		0-19	20-39	40-59	60-79	80-89	100-119 120-140
29 Mar	1	13					
	4/5						2
21 Apr	1	46	78				
	4/5						16
25 Jun	1		21	24	5		
	4/5						20
5 Jul	1			6	9	9	1
	3					9	
	4					1	12
	5					2	17
22-28 Aug	1			2	18	5	
	2				1	13	
	3						14 1
	4					1	8
	5						7 1
2 Dec	1				1	2	
	4					14	11 4

Table 5.—Seasonal variation in number and size (SVL) of salamanders in each breeding stage collected from Bodie Canyon Tank.

Date	Stage	Snout/Vent Length (mm)					
		0-19	20-39	40-59	60-79	80-89	100-119 120-140
28 Mar	1	10	74	21			
	3						10 7
25 Aug	1				18	21	
	2				3	18	
	3						2
	4						3 2
26-27 Sep	2						2 3
	3					8	6 1
	4						3 4
11 Nov	3					2	1 1
	4					2	

zona Game and Fish Commission order #R12-4-311. Enforcement is difficult, because SRV is large and sparsely settled. It would be easy to introduce exotic *A. tigrinum* into this valley. Pre-mating and post-mating isolating mechanisms in the *A. tigrinum* species group within *Ambystoma* are weak (Brandon 1972, Nelson and Humphrey 1972).

Introduced *A. tigrinum* would be expected, therefore, to easily interbreed with native tiger salamanders.

Discussion

In theory, average heterozygosity or gene diversity of organisms in an area can be decomposed into gene diversities within and between any subpopulations comprising the total number of organisms in the population (Nei 1987). If all organisms in a population are a panmictic aggregate, then the component describing variation between subpopulations is zero. We have no information on dispersal between tanks in SRV, so for this discussion we arbitrarily consider each tank a subpopulation and together all tanks comprise the total population of SRV salamanders. Within this context our results highlight several factors to consider in trying to understand the evolutionary genetics of SRV tiger salamanders.

Mean heterozygosity (.0015) for *A. t. stebbinsi* is the lowest reported for any salamander (Jones et al. 1988). Salamanders in SRV went through one or more bottlenecks at some point in their history, but cause(s) and time of reduction in numbers and associated genetic diversity are unknown. The effect of a one-time bottleneck is a drastic decrease in expected heterozygosity of a population, and in theory, repeated bottlenecks could reduce gene diversity even more (Motro and Thomson 1982).

Current factors affecting changes in SRV salamander numbers may

provide some insight into the origin and/or perhaps maintenance of low gene diversity in SRV. Increased heterozygosity generally correlates positively with traits associated with high individual vigor and fitness, plus population stability (Mitton and Grant 1984). Susceptibility to disease or apparent reduced ability to overcome infection may thus be consequences of reduced genetic variation in SRV salamanders. A historical bottleneck in population size with associated loss of gene diversity in SRV salamanders, therefore, could have resulted in populations more susceptible to disease. This susceptibility, as seen in contemporary stocktanks, could easily cause severe reductions in numbers of salamanders and retard any expected increase in gene diversity. O'Brien et al. (1985) provide a related example. They describe how extremely low genetic variation in the South African cheetah may derive from a population

bottleneck. Low genetic variation seen in structural loci also extends to the major histocompatibility complex. This extreme monomorphism correlates with a hypersensitivity in cheetahs to some viral pathogens, and they feel the sensitivity of this genetically uniform species to pathogens provides an example of the protection against disease genetic variation provides to species. The mechanism connecting low genetic variation revealed by electrophoresis and susceptibility to disease is unclear. Hence, for both cheetahs and SRV salamanders it is uncertain if reduction of population size and loss of genetic variation increased susceptibility to disease, or alternatively, susceptibility increased for some other reason, and this lead to reductions in population numbers.

Two additional factors, again found in present stocktanks, would reinforce this pattern of change in numbers of salamanders and reduc-

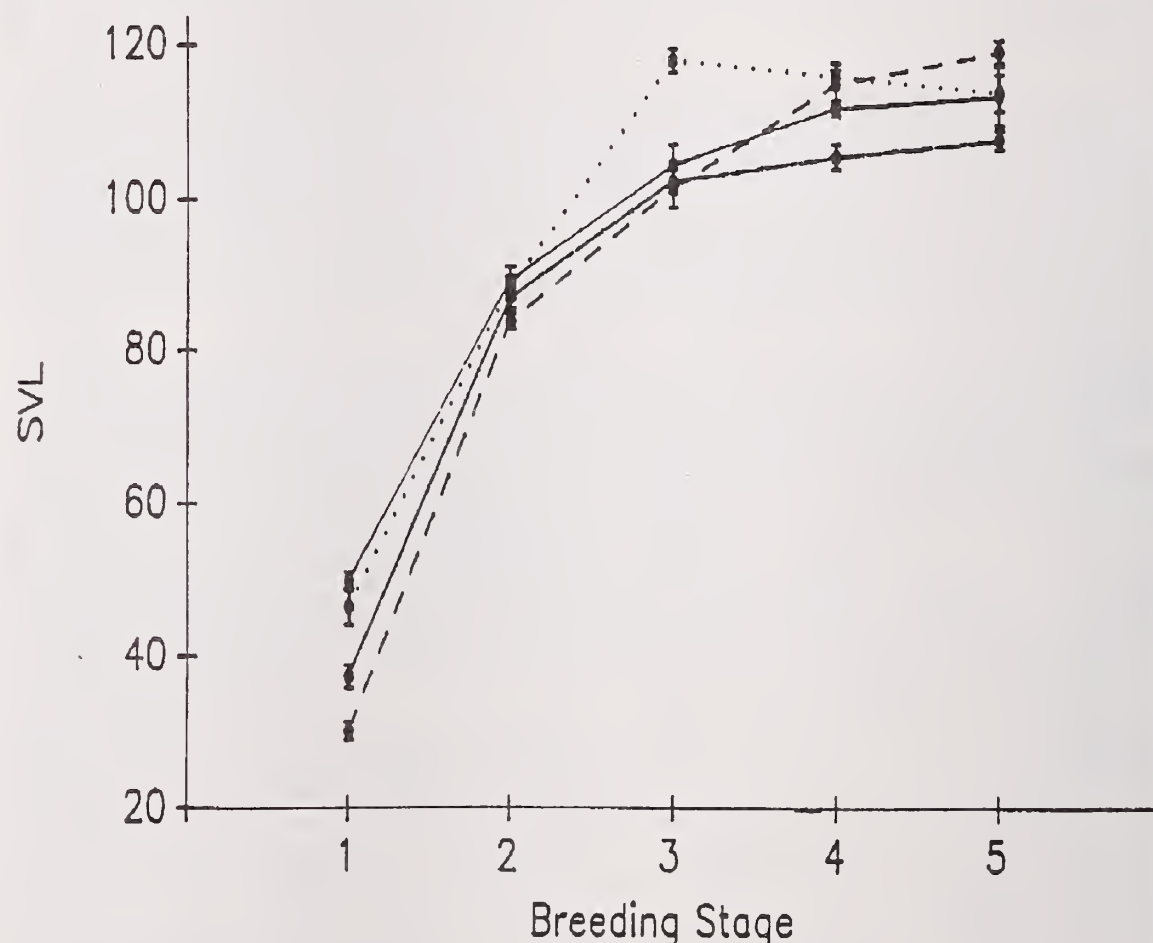


Figure 2.—Variation in SVL with breeding stage for animals from four SRV populations: solid line=Upper 13 Reservoir, dotted line=Parker Canyon Tank #1, dots+dashes=Huachuca Tank, dashes=Bodle Canyon Tank. (Circles=mean, vertical line=1SE, perpendicular horizontal line=limits.)

tion in heterozygosity. First, in SRV, most salamanders occur in aquatic habitats and most, if not all, salamanders in the water at the time of an epidemic are apparently killed. Since most SRV salamanders are adult, branchiate animals, aquatic disease dramatically reduces effective population size. Furthermore, future population recruitment is reduced

since a larval year class is also lost. Thus, the preponderance of branchiate morphs in SRV subpopulations exacerbates any negative effects of aquatic diseases on population size and heterozygosity. If disease is a predictable selection pressure, however, it is not obvious why relative frequency of adult morphs in a subpopulation has not shifted from

branchiate to metamorphosed morphs. Since disease appears to equally affect metamorphosed and branchiate morphs, this may indicate there is little or negligible difference in heritable variation for disease resistance between morphs. Selection, therefore, would have little or no effect on relative morph frequencies. Likewise, the genetic basis of paedomorphosis versus metamorphosis is poorly understood. It may be that genetic differences between morphs are slight, with environmental conditions largely determining relative frequency of each adult morph in a subpopulation.

Second, exotic predaceous fishes, like an aquatic-borne disease, will quickly reduce adult and larval salamander numbers, and coincidentally genetic diversity, in any stocktank in which they are introduced. Haphazard introduction of fishes in SRV habitats may help maintain low levels of genetic diversity.

Other than by mutation, heterozygosity in SRV could be increased by the introduction of exotic *A. tigrinum*, and their interbreeding with native SRV salamanders. The only report on salamander introductions in AZ is 20 yrs old, summarizes use of salamanders as bait in only the extreme western part of AZ, and provides no information on relative numbers imported into AZ, as opposed to salamanders moved within AZ (Espinoza et al. 1970). Nonetheless, in 1968, about 2.5 million salamanders in western AZ were available for potential introduction into aquatic habitats. The increased number of people living in AZ means these numbers are probably higher now. Furthermore, salamanders are regularly sold for bait in all major population centers in AZ, not just along the Colorado River. Salamanders sold in AZ come from three primary sources: (1) seined from AZ populations; (2) collected and imported from populations in at least NM, OK, CO, TX, and NE; and (3) adults and/or larvae collected in AZ or other states, intro-

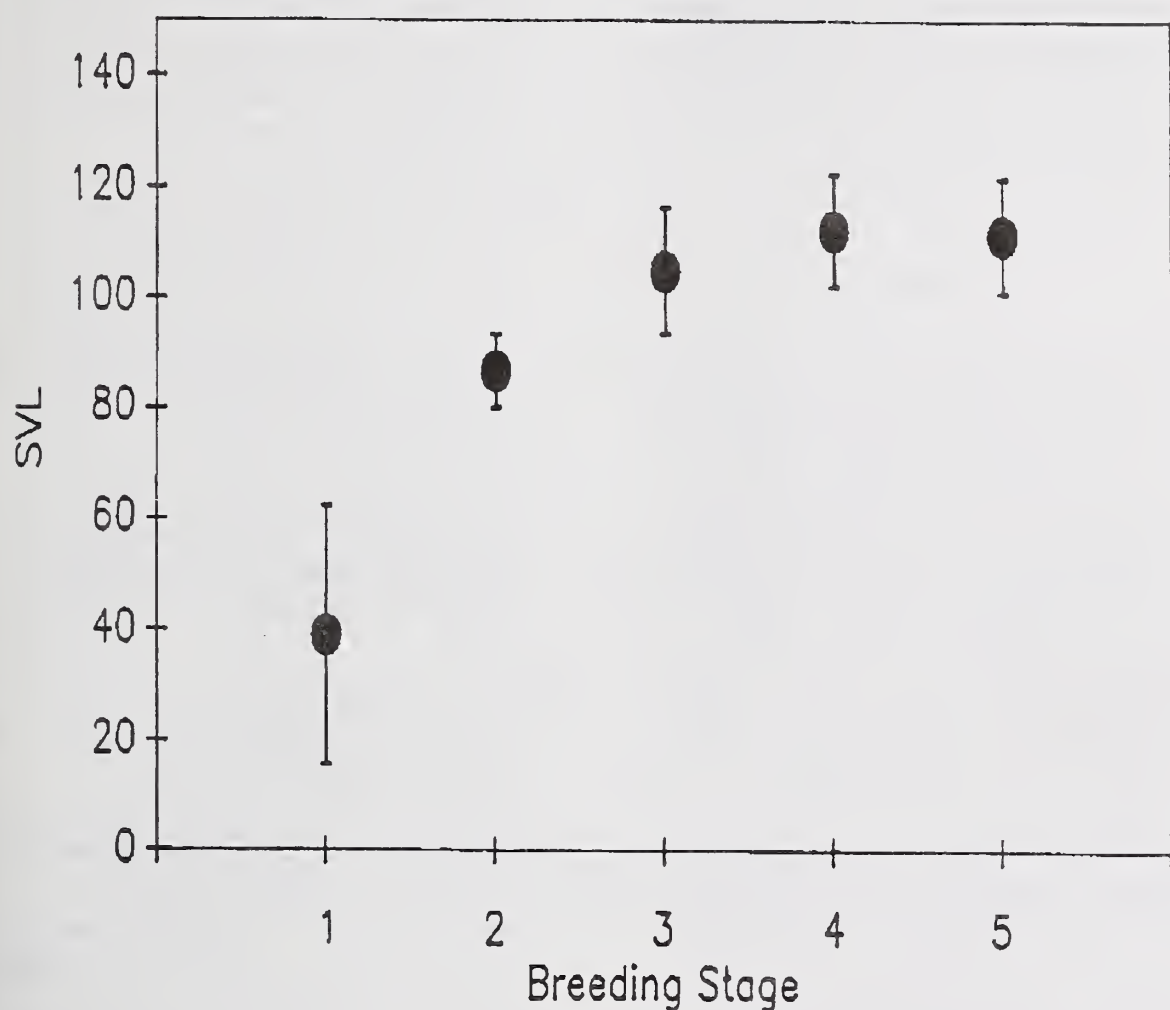


Figure 3.—Variation in SVL with breeding stage for all SRV populations. Symbols as in figure 2.

Table 6.—Total bait sales in the Lower Colorado River basin (modified after Espinoza et al. 1970).

Area	Value of sales (\$)	Volume of sales	
		Salamanders	Minnows
1. Las Vegas-Lake Mead	190,000	1,250,000	750,000
2. Mid-river	110,000	570,000	325,000
3. Parker Dam	80,000	400,000	185,000
4. Yuma	53,000	190,000	290,000
5. Blythe-Palo Verde	24,000	30,000	230,000
Total in 1968	457,000	2,440,000	1,780,000

duced into AZ habitats as "brood stock," and larvae from these animals collected in subsequent years and sold as bait.

We know from discussions with residents that salamanders are at least occasionally moved between tanks in SRV. We have no evidence salamanders are introduced into SRV from elsewhere, and two facts suggest such events are rare or non-existent. First, our electrophoretic data show heterozygosity is uniformly low for SRV animals from eight subpopulations separated by as much as 25 km (fig. 1) (Jones et al. 1988). Allelic diversity should be higher if salamanders are regularly being introduced into SRV. Second, there is only one mitochondrial DNA clone in SRV. Again, regular introductions would be expected to result in more than one mtDNA haplotype in SRV. Nonetheless, continued active use of salamanders for bait in AZ means there is always the possibility exotic animals might be introduced. This could lead to introgressive hybridization between species or subspecies, or perhaps interbreeding between genetically distinctive populations of the same species. Furthermore, we cannot completely exclude the possibility that *A. t. nebulosum* and/or *A. t. mavortium* was deliberately or accidentally introduced into SRV, thus creating the opportunity for hybridization between these races. However, several arguments suggest salamanders were native in SRV (Jones et al. 1988).

Among tiger salamanders in SRV, color pattern of metamorphosed animals, relative frequency of typical and cannibal morphs, nuclear gene frequencies derived from electrophoresis, and mitochondrial DNA genotype each show distinctive variation relative to the entire *A. tigrinum* complex. We conclude, therefore, that SRV tiger salamander populations are sufficiently different to warrant at least subspecific status as *A. t. stebbinsi* (Collins 1988, Jones et al. 1988). Likewise, the small number

and restricted geographic range of SRV populations increases their likelihood of extinction. These facts coupled with our information concerning life history, incidence of disease, and potential negative effects of exotic animals in SRV, argue that conservation efforts and careful management of *A. t. stebbinsi* is needed. Although *A. tigrinum* has a wide distribution, in some races special effort needs to be directed at protecting locally adapted populations to conserve the diversity of genetic and life history traits characteristic of this polytypic species.

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Appendix

Locality data for all populations of *A. t. stebbinsi*, taken from the following U.S.G.S. 7½ min. quadrangles: Campini Mesa, Canelo Pass, Duquesne, Harshaw, Huachuca Peak, Lochiel.

Site	Locality	Map codes	Site	Locality	Map codes
Bodie Canyon Tank:	NW • SE • sec.2, T.24S, R.18E 31° 22' 30"N, 110° 28' 45"W	8	Inez Tank:	SW • NW • sec.2, T.24S, R.18E 31° 22' 30"N, 110° 29' 30"W	D
Bog Hole Tank:	NW • SE • sec.33, T.22S, R.17E 31° 28' 36"N, 110° 37' 06"W	F	Judy Tank:	SE • SE • sec.35, T.23S, R.18E 31° 23' 04"N, 110° 29' 19"W	9
Campini Mesa Tank #1:	SW • E • sec.19, T.24S, R.19E 31° 21' 00", 110° 26' 45"W		Ki-He-Kah Ranch Tank:	SW • SW • sec.1, T.23S, R.17E 31° 26' 26"N, 110° 35' 22"W	
FS 58 Tank:	NE • NE • sec.6, T.23S, R.17E 31° 27' 03"N, 110° 38' 49"W	F	Lower 13 Reservoir:	SW • NE • sec.18, T.24S, R.17E 31° 20' 49"N, 110° 39' 05"W	
FS 799 Tank:	SW • NE • sec.36, T.22S, R.17E 31° 28' 48"N, 110° 34' 09"W	7	Meadow Valley Flat Tank #1	SW • NE • sec.6, T.22S, R.17E 31° 27' 49"N, 110° 38' 47"W	1
Grennan Tank:	S center sec.14, T.23S, R.16E 31° 25' 29"N, 110° 40' 47"W	6	Parker Canyon Tank #1:	NE • NE • sec.19, T.24S, R.18E 31° 20' 16"N, 110° 32' 42"W	2,D
Heron Springs Tank:	SW • NE • sec.14, T.24S, R.17E 31° 20' 39"N, 110° 34' 54"W		School Canyon Tank #1:	NE • SE • sec.9, T.24S, R.18E 31° 21' 28"N, 110° 24' 04"W	4
Huachuca Tank:	NE • NW • sec.15, T.24S, R.18E 31° 21' 12"N, 110° 30' 15"W	3,F,D	School Canyon Tank #2:	NE • SE • sec.17, T.24S, R.19E 31° 21' 14"N, 110° 24' 24"W	
			Upper 13 Reservoir:	S center sec.7, T.24S, R.17E. 31° 21' 18"N, 110° 39' 16"W	5

Habitat Requirements of New Mexico's Endangered Salamanders¹

Cynthia A. Ramotnik² and Norman J. Scott, Jr.³

Two of the three species of salamanders that occur in New Mexico are restricted to coniferous forests at high elevations. The Jemez Mountains salamander (*Plethodon neomexicanus*) (fig. 1) is known only from north-central New Mexico at the southern terminus of the Rocky Mountains (Reagan 1972). The Sacramento Mountain salamander (*Aneides hardii*) (fig. 2) occurs in the Capitan and Sacramento Mountains in south-central New Mexico (Williams 1976). These lungless salamanders, with small body sizes and terrestrial juvenile development, are restricted to mesic environments. Lowe (1950) suggested that both species are relicts of the mid-Tertiary Rocky Mountain fauna.

In 1975, both species were listed by the state of New Mexico as endangered due to their restricted distribution (Hubbard et al. 1979). Since 1980, increases in timber harvest by

the U.S. Forest Service (USFS) and changes in timber practices have prompted concern about the effect of logging on these salamanders (Scott et al. 1987, U.S. Fish & Wildlife Service 1986). Most of the range of each species occurs on National Forest (NF) lands, and the close association of these salamanders with mixed coniferous forests may make them vulnerable to some forest-management practices. In 1985, both species were placed under review as potentially threatened or endangered species under the Federal Endangered Species Act (Ramotnik 1986, Staub 1986). As a result, an interagency committee was established to identify data and management needs and develop strategies to address these needs.



Figure 1.—Jemez Mountain salamander (*Plethodon neomexicanus*). Photo by Stephen Corn.

Abstract.—We measured habitat components for two state-listed endangered salamanders in New Mexico in 1986 and 1987. Both species are restricted to mesic environments within high-elevation, mixed coniferous forests. Steep slope and high elevation were the most useful variables for predicting the occurrence of Jemez Mountains salamanders and Sacramento Mountain salamanders, respectively. Although the discriminant models show some predictive value in detecting salamanders based on habitat variables, we believe that the best survey technique is ground-truth surveys in wet weather. A better fit of the discriminant models might be obtained by including variables not measured e.g., fire and logging history, and soil characteristics. We offer interim management guidelines as a result of our analysis.

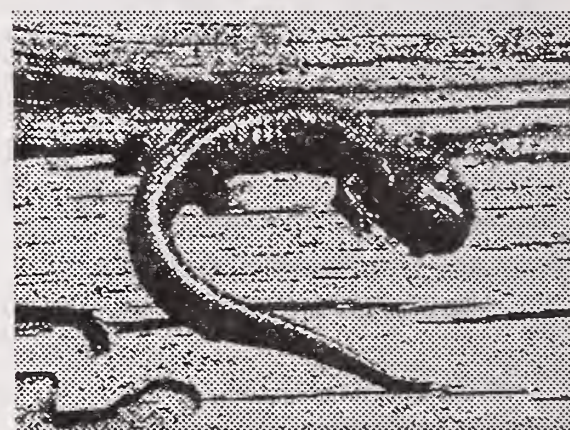


Figure 2.—Sacramento Mountain salamander (*Aneides hardii*). Photo by Stephen Corn.

In 1986, the U.S. Fish & Wildlife Service (USFWS) contracted with the USFS to study these species on NF lands. The primary objectives were to survey for salamanders in planning units under consideration for future logging operations and to characterize salamander habitats using habitat components that are meaningful and useful to USFS biologists and land managers. This information would be used to assess potential salamander habitat from maps or aerial photos, thereby reducing the need to inventory areas by ground-truth assessment.

In this paper, we characterize habitats of Jemez Mountains salamanders and Sacramento Mountain salamanders based on general site characteristics and surface cover

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items that could serve as refugia for salamanders. We use a multivariate analysis of habitat characteristics that describes areas with and without salamanders, and present management guidelines as a result of this analysis.

Study Areas

We studied the Jemez Mountains salamander within the Santa Fe NF in the Jemez Mountains (Los Alamos, Rio Arriba, and Sandoval Counties, New Mexico), which are located approximately 100 km north of Albuquerque (fig. 3). The Jemez Mountains are volcanic in origin and are underlain by volcanic rock, ash, and pumice. The predominant feature in the area is the volcanic caldera, the Valle Grande, around which the mountains lie. Fieldwork on the Sacramento Mountain salamander was conducted in the Sacramento Mountains, within the Lincoln NF, Otero County, New Mexico (fig. 3). Volcanic intrusions occur within the Paleozoic strata of the Sacramento Mountains. Elevations in the Jemez Mountains range from 2130-3410 m, and from 2290-3600 m in the Sacramento Mountains.

Habitat types within these elevational ranges occur within the Rocky Mountain upper montane (2290-2900 m) and subalpine (2900-3660 m) forest association (Castetter 1956). The upper montane forest association (Shelford 1963) is characterized by mixed coniferous forests dominated by white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and blue spruce (*Picea pungens*). Deciduous components include quaking aspen (*Populus tremuloides*), Rocky Mountain maple (*Acer glabrum*), oak (*Quercus* spp.), New Mexico locust (*Robinia neomexicana*), and oceanspray (*Holodiscus dumosus*). Ponderosa pine (*Pinus ponderosa*) stands predominate at the lower elevations, particularly on south-facing slopes. Within the

subalpine forest association, Engelmann spruce, Douglas-fir, and white fir are the most common trees. Aspen and Rocky Mountain maple are found to a lesser extent. Aspen groves, talus fields, and open meadows are present at higher elevations. Annual precipitation in the Jemez Mountains ranges from 400-550 mm (Castetter 1956) and is slightly higher in the Sacramento Mountains. Much of the precipitation falls between July and September (Kunkel 1984).

Methods

We conducted fieldwork in the summers of 1986 and 1987 (Jemez Mountains: 28 July-14 August 1986, 29 June-11 July 1987, 24 August-5 September 1987; Sacramento Mountains: 22 August-10 September 1986, 8-20 June 1987; 20 July-1 August 1987). These dates included the surface activity periods of Jemez Mountains salamanders (Reagan 1972) and Sacramento Mountain salamanders (Williams 1976).

Transects were established in forested areas; most were located in planning units selected by USFS personnel. Within these areas, locations of transects were selected from topographic maps to sample a variety of topographic aspects. South-facing slopes were not searched in the Jemez Mountains due to the difficulty in locating salamanders on these slopes (Ramotnik 1988). To ensure having sites occupied by salamanders, we visited known localities or areas where salamanders had recently been found. A small number of sites outside planning units were chosen from topographic maps.

We established 100-m² transects (2 m x 50 m) oriented uphill from near the bottoms of slopes. Our transect is modified from area-constrained searches, a technique developed by others, e.g., Bury (1983), Bury and Corn (this volume), Bury and Raphael (1983), Campbell and Christman (1982), Raphael (this volume),

and Raphael and Rosenberg (1983). The areas of four classes of cover items (rock, bark, fine woody debris, and coarse woody debris) were estimated visually. We further divided coarse woody debris (CWD) into three decay classes, adapted from a five-class scheme for rating decomposition of Douglas-fir logs (Franklin et al. 1981). To emphasize differences between decay classes, we combined classes 1 and 2 (CWD1), and classes 3 and 4 (CWD3), and placed the most decayed logs, class 5, in a third category (CWD5).

Aspect was taken with a magnetic compass at 10, 30, and 50 m. Compass readings were assigned to one of four aspect classes where 316-45° = north-facing; 46-135° = east-facing; 136-225° = south-facing; and 226-315° = west-facing. Percent slope was determined with a clinometer, and percent canopy cover was estimated with a spherical densiometer (Lemmon 1956). Both measurements were recorded at 10-m intervals. All readings were made along the transect and averaged for the

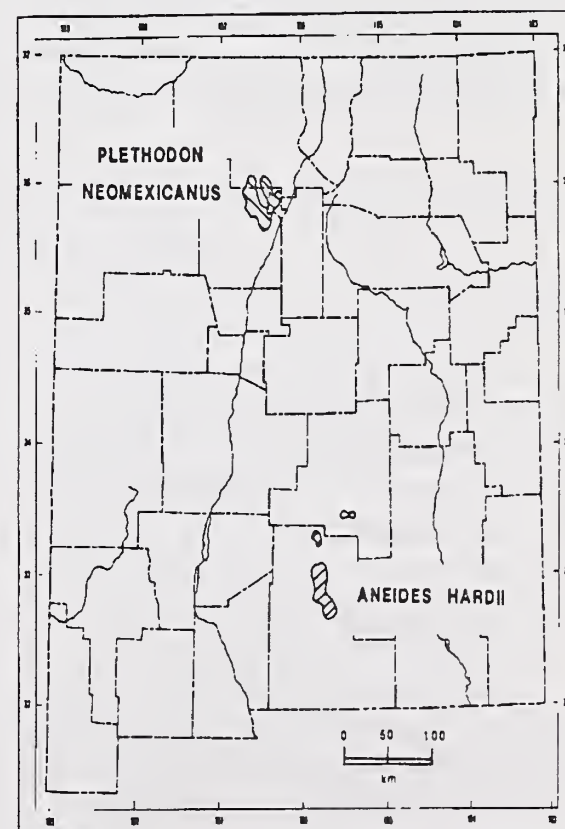


Figure 3.—Distribution of Jemez Mountains salamanders (*Plethodon neomexicanus*) and Sacramento Mountain salamanders (*Aneides hardii*) in New Mexico.

transect. Numbers of white fir and Douglas-fir were pooled in a single class (TFIR), as were Engelmann and blue spruce (TSPRUCE), and *Pinus* spp. (TPINE). Numbers of trees within tree classes were counted in a 20-m x 50-m plot centered over the transect. Twenty-three measured and derived variables were used in the analyses (table 1).

We determined numbers of salamanders on transects by searching all cover items manually or with potato rakes. The locations of salamanders in other than the four classes of cover items also were recorded. When a salamander was found, we recorded snout-vent length (distance from tip of snout to anterior edge of vent), sex, and dimensions and type of cover item. For coniferous logs, we also recorded salamander position relative to the log (in, under, or under bark) and decay class (modified from Corn and Bury, in press, Raphael and Rosenberg 1983). These data were used to calculate densities of salamanders on transects and to determine cover item use by salamanders. We acquired additional data on cover item use by salamanders by locating salamanders in areas on both sides of the transects.

Statistical Analysis

Data for transects with and without salamanders were pooled separately. We calculated descriptive statistics (mean, standard error, range) for habitat variables in the two groups and used a one-way analysis of variance to compare transformed variables between groups. Size classes of fir and spruce were compared between the two groups with a t-test.

The following transformations were applied to stabilize the variance of the habitat variables (Snedecor and Cochran 1967) and to increase the probability of a normal distribution: arcsine (SLOPE CANOPY); square root + 0.5 (tree densities); and log + 0.5 (cover items). Elevation was

not transformed because values were distributed normally.

A stepwise variable entry procedure (STEPDISC) selected the "best set" of habitat variables to discriminate between groups and reduced the complexity of the original variable set. Because the models selected by STEPDISC are not necessarily the best possible models (SAS Institute Inc 1982), cross-validation was accomplished by using canonical analysis (CANDISC) or descriptive discriminant analysis (DDA) (Williams 1983). DDA attempts to establish op-

timal separation between groups using linear transformations of the independent variables based on variables selected by the stepwise procedure. The Mahalanobis distance between group means was tested using an F-statistic.

Predictive discriminant analysis (PDA) (Williams 1983) (DISCRIM) was used to test the discriminatory power of the variables selected by DDA. We used chi-square analysis to compare cover item use (of the four classes) to availability and to compare aspects of transects with and

Table 1.—Description of measured and derived habitat variables used in habitat selection analysis of two species of New Mexico salamanders.

Sampling unit mnemonic	Description
<i>50-m x 2-m transect</i>	
BARK	Estimate of amount of bark on ground (m ²)
CANOPY	Average percent canopy cover recorded with a spherical densiometer
CWD1	Estimate of amount of poorly decayed coarse woody debris (m ²)
CWD3	Estimate of amount of moderately decayed coarse woody debris (m ²)
CWD5	Estimate of amount of well-decayed coarse woody debris (m ²)
CWD	CWD1 + CWD3 + CWD5
ELEV	Estimated from a U.S. Geological Survey topographic map (m)
FWD	Estimate of amount of fine woody debris (sticks) (m ²)
ROCK	Estimate of amount of surface rock (m ²)
SLOPE	Average percent slope measured with a clinometer
<i>50-m x 20-m plot</i>	
SFIR	Number of small fir (<20 cm dbh)
MFIR	Number of medium fir (20-50 cm dbh)
LFIR	Number of large fir (>50 cm dbh)
TFIR	SFIR + MFIR + LFIR
SSPRUCE	Number of small spruce (<20 cm dbh)
MSPRUCE	Number of medium spruce (20-50 cm dbh)
LSPRUCE	Number of large spruce (>50 cm dbh)
TSPRUCE	SSPRUCE + MSPRUCE + LSPRUCE
TASPEN	Number of aspen (all sizes)
TNOD	Number of non-oak deciduous (all sizes)
TOAK	Number of oak (all sizes)
TPINE	Number of pine (all sizes)
TSNAGS	Number of snags (all sizes)

without salamanders. The Statistical Analysis System computer package (SAS, Version 5) was used for all analyses (SAS Institute Inc 1982). Significance levels were set at $P < 0.05$ unless otherwise indicated.

Results

Jemez Mountains Salamander

Salamanders ($N = 28$) were present on 10 of 43 transects (23%) with a mean density of 3/100 m² in occupied areas. One hundred twenty salamanders were found in areas off the transects. Transects with salamanders occurred on significantly steeper slopes and at lower elevations than transects without salamanders (table 2). Analysis of size classes of fir and spruce showed no significant differences between transects with and without salamanders. Proportions of decay classes of CWD

also did not differ significantly between the two groups of transects ($X^2 = 0.28$, $df = 2$, $P > 0.90$). The amount of CWD1 was similar between groups but amounts of CWD3 and CWD5 were higher on transects with salamanders. Although no south-facing slopes were searched, proportions of other aspects occupied by salamanders were not different from the proportions of total aspects searched ($X^2 = 1.3$, $df = 2$, $P > 0.50$).

Three of the original 20 variables were selected by the stepwise variable entry procedure for inclusion in the descriptive discriminant model: SLOPE, TPINE, and LSPRUCE (table 3). Subsequent analysis by DDA retained these variables. The resultant discriminant function explained 38% of the between-group variance; however, it did not have significant power in discriminating between groups ($F = 2.34$, $P = 0.09$). This function describes a multivariate gradient that ranges from steep slopes with

many pine and large spruce trees containing salamanders, to shallow slopes with few pine or large spruce trees without salamanders. SLOPE had the highest discriminating power ($r^2 = 0.73$). PDA correctly classified 91% of the 33 transects without salamanders and 80% of the 10 transects with salamanders.

The 10 transects and additional searches produced 148 Jemez Mountains salamanders; the type of cover item was known for all but one salamander. Ninety-six percent (141/147) of salamanders were distributed among the four major cover classes as follows: CWD, 100 (68%); ROCK, 40 (27%); FWD, 1 (1%). No salamanders were found under BARK. Three salamanders (2%) were found on transects under surface litter and three salamanders (2%) were found under aspen logs. The frequency of salamanders associated with CWD by decay class was CWD1—4%; CWD3—66%; CWD5—30%. Of 28 salamanders found on transects, 24 salamanders were associated with one of the four classes of cover items. Because of the small sample size, we were unable to determine a correlation between cover item availability and use.

Table 2.—Comparison of habitat variables measured on transects with and without Jemez Mountains salamanders, Santa Fe National Forest, 1986-1987. Significance is based on one-way analysis of variance. Mnemonic codes for habitat variables are explained in table 1.

Mnemonic	Transects (N = 10) with salamanders $\bar{x} \pm se$ (range)		Transects (N = 33) without salamanders $\bar{x} \pm se$ (range)		Significance
ELEV	2526	± 35.8 (2359-2621)	2635	± 22.0 (2332-2886)	*
SLOPE	66	± 2.5 (55-84)	44	± 2.8 (0-82)	**
CANOPY	62	± 1.8 (56-65) ¹	64	± 2.1 (21-82) ²	NS
TFIR	72	± 10.4 (29-156)	95	± 10.3 (22-292)	NS
TSPRUCE	17	± 6.6 (0-59)	20	± 5.9 (0-163)	NS
TPINE	25	± 7.8 (0-63)	9	± 2.1 (0-56)	NS
TASPEN	20	± 8.8 (1-96)	17	± 2.5 (0-60)	NS
TOAK	10	± 6.6 (0-59)	7	± 2.4 (0-50)	NS
TSNAGS	33	± 6.1 (5-64)	27	± 3.3 (3-82)	NS
TNOD	29	± 10.4 (0-103)	8	± 2.0 (0-51)	NS
ROCK	11	± 2.6 (3-26)	7	± 1.6 (0-37)	NS
FWD	4	± 1.1 (2-12)	4	± 0.5 (0-15)	NS
BARK	1	± 1.0 (0-10)	1	± 0.1 (0-3)	NS
CWD	10	± 1.9 (1-20)	9	± 0.8 (1-26)	NS

* $P < 0.05$

** $P < 0.005$

¹Data are available for 5 transects.

²Data are available for 29 transects.

Sacramento Mountain Salamander

Salamanders ($N = 233$) were present on 26 of 80 transects (33%) with a mean density of 6/100 m² in occupied areas. We located 387 salamanders in areas off the transects.

Transects with and without salamanders differed in several respects: transects with salamanders occurred at significantly higher elevations, on shallower slopes, and had higher numbers of spruce and lower numbers of pine than transects without salamanders (table 4). Analysis of size classes of fir and spruce revealed that densities of large fir and all size classes of spruce were significantly higher on transects with salamanders

(LFIR: $t = 3.38$, $P = 0.001$; SSPRUCE: $t = 2.85$, $P = 0.008$; MSPRUCE: $t = 2.56$, $P = 0.016$; LSPRUCE: $t = 3.04$, $P = 0.003$) (fig. 4). Although the total amount of CWD on transects with and without salamanders was not significantly different, there was significantly more CWD5 on transects with salamanders ($X^2 = 6.93$, $df = 2$, $P > 0.05$). The proportions of transects by aspect did not differ between the two groups ($X^2 = 3.83$, $df = 3$, $P > 0.10$).

Because numbers of the three size classes of spruce were significantly higher on transects with salamanders, we substituted TSPRUCE for SSPRUCE, MSPRUCE, and LSPRUCE in subsequent analyses. A stepwise variable entry procedure selected eight of the original 20 variables for inclusion in the descriptive discriminant model (table 5). Subsequent DDA kept all but three (SLOPE, CWD1, and TAPSEN) in the model. The resultant discriminant function explained 49% of the between-group variance and had significant power in discriminating between groups ($F = 6.87$, $P < 0.0001$). This function can be interpreted ecologically to describe a gradient that ranges from low elevations with many pine, few spruce and large fir, and infrequent CWD5 without salamanders, to higher elevations, few pine, many spruce and large fir, and abundant CWD5 that contain salamanders. ELEV had the highest discriminating power ($r^2 = 0.64$). PDA correctly classified 96% of the 54 transects without salamanders and 58% of the 26 transects with salamanders.

The 26 occupied transects and additional searches produced 620 Sacramento Mountain salamanders. Ninety-five percent (589) were distributed among the four major cover classes as follows: CWD, 377 (64%); ROCK, 127 (22%); BARK, 58 (10%); and FWD, 27 (4%). Fourteen salamanders (2%) were found under aspen logs and 17 salamanders (3%) were above or below surface litter.

The frequency of salamanders associated with CWD in the three decay classes was CWD1—13%; CWD3—62%; CWD5—25%. Of 233 salamanders found on transects, 209 salamanders were associated with one of the four classes of cover items. Examination of cover item availability and use for these salamanders revealed that salamanders are associated with some cover items disproportionate to their availability ($X^2 = 59.9$, $df = 3$, $P < 0.001$). In particular, *Aneides* was found in association with FWD proportionately less frequent than expected, and used well-decayed and moderately decayed logs to a greater extent than expected ($X^2 = 62.1$, $df = 2$, $P < 0.001$).

Discussion

Jemez Mountains Salamander

While canonical analysis did not discriminate between transects with and

without salamanders, it did identify steep slopes as the most useful variable in determining the occurrence of Jemez Mountains salamanders. It is possible that steep slopes contain more interstitial spaces in the soil than do shallower slopes. The soils of steep slopes may be less compacted than those of more gentle slopes due to the combined effects of gravity, and movement of water and soil. As a consequence of steep slope and the presence of underlying volcanic rock characteristic of the Jemez Mountains (Burton 1982), spaces within this ma-

Table 3.—Correlations of habitat variables with discriminant scores for transects with and without Jemez Mountains salamanders.

Mnemonic	DF1
SLOPE	0.73
TPINE	0.52
LSPRUCE	0.35

Table 4.—Comparison of habitat variables measured on transects with and without Sacramento Mountain salamanders, Lincoln National Forest, 1986-1987. Significance is based on one-way analysis of variance. Mnemonic codes for habitat variables are explained in Table 1.

Mnemonic	Transects (N = 26) with salamanders $\bar{x} \pm se$ (Range)		Transects (N = 54) without salamanders $\bar{x} \pm se$ (Range)		Significance
ELEV	2779	± 17.6 (2618-2890)	2682	± 8.7 (2450-2792)	**
SLOPE	39	± 2.7 (21-65)	41	± 1.6 (17-70)	**
CANOPY	72	± 1.3 (59-88)	71	± 1.3 (53-90)	NS
TFIR	67	± 6.3 (8-122)	64	± 4.0 (14-144)	NS
TSPRUCE	17	± 7.6 (0-186)	1	± 0.6 (0-30)	**
TPINE	7	± 2.1 (0-50)	22	± 2.3 (0-71)	*
TASPEN	14	± 4.1 (0-74)	17	± 3.3 (0-107)	NS
TOAK	5	± 2.4 (0-59)	18	± 3.8 (0-104)	NS
TSNAGS	24	± 2.8 (6-56)	25	± 2.5 (1-106)	NS
TNOD	33	± 7.7 (4-180)	34	± 5.6 (0-222)	NS
ROCK	7	± 1.7 (0-33)	7	± 0.9 (0-29)	NS
FWD	6	± 0.6 (2-13)	5	± 0.5 (0-14)	NS
BARK	1	± 0.3 (0-6)	1	± 0.2 (0-10)	NS
CWD	12	± 1.2 (4-24)	8	± 0.8 (0-26)	NS

** $P < 0.005$

* $P < 0.05$

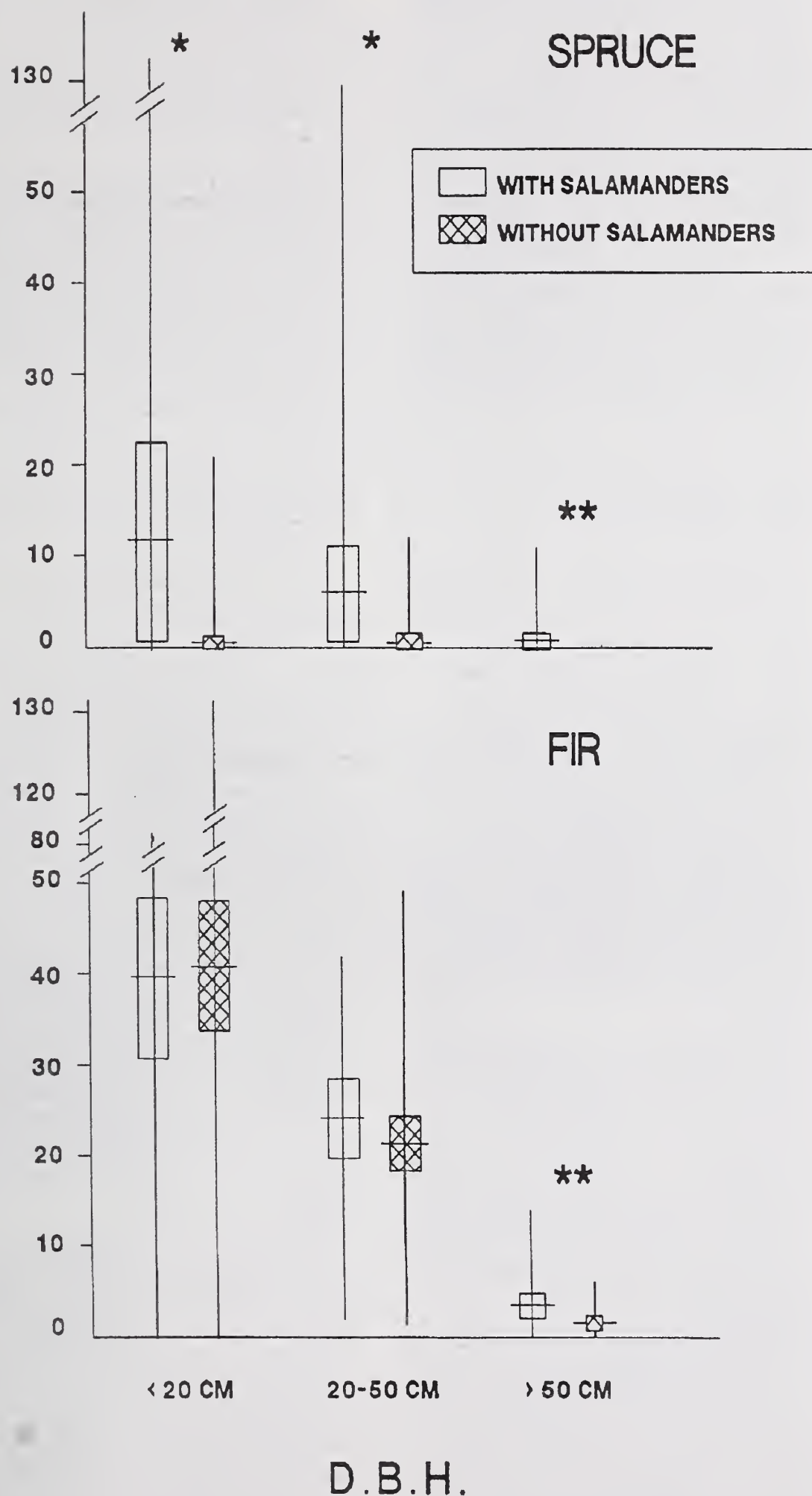


Figure 4.—Comparisons of average size classes (d.b.h.) of spruce and fir on transects with and without Sacramento Mountain salamanders. Boxes indicate 95% confidence intervals for the mean. Levels of significance indicated by asterisks are 0.05 (*) and 0.005 (**).

trix of rocky soil may provide refugia for salamanders during inhospitable times and, thus, may provide a clue to the survival of this salamander in the harsh environment of the Rocky Mountains. The largest concentrations of *P. neomexicanus* have been found in association with talus slopes (Whitford and Ludwig 1975, Clyde Jones pers. comm.), which are also important to many other western *Plethodon* (Brodie 1970). Other plethodontids are virtually restricted to areas with a loose rocky soil (Aubry et al. 1987, French and Mount 1978, Herrington and Larsen 1985, Jaeger 1971).

The variables selected by canonical analysis showed some predictive value. Although three transects without salamanders were misclassified by PDA as transects with salamanders, *Plethodon* was found in areas adjacent to the transects. The two transects misclassified as transects without salamanders had values for TPINE and LSPRUCE closer to values usually associated with transects without salamanders. Because a larger percentage of transects without salamanders were correctly classified by PDA, these three variables may better describe the conditions under which salamanders are absent from an area, rather than describing favorable conditions under which they would occur.

The limited discriminatory and predictive power of the variables se-

Table 5.—Correlations of habitat variables with discriminant scores for transects with and without Sacramento Mountain salamanders.

Mnemonic	DF1
ELEV	0.55
TSPRUCE	0.42
TPINE	-0.47
CWD5	0.44
LFIR	0.34
CWD1	-0.05
SLOPE	-0.06
TASPEN	-0.02

lected by multivariate techniques may reflect our inability to reliably and consistently detect the presence of *Plethodon* at a site. We believe that our ability to detect salamanders is fairly good and repeatable, but we realize that environmental factors can influence the relative numbers of salamanders. During repeated visits to the same sites, *Plethodon* was more abundant when we searched under wet conditions, and other studies have reported a significant correlation between movement and activity of salamanders, and precipitation (Barbour et al. 1969, Kleeberger and Werner 1982, MacCullough and Bider 1975). Low densities and patchiness of *P. neomexicanus* populations also can hinder detection of the animal. In comparison with densities of red-backed salamanders, *P. cinereus*, (0.9-2.2 individuals/m²; Heatwole 1962, Jaeger 1980), our density estimates for Jemez Mountains salamanders are extremely low (0.03 individuals/m²). Although Williams (1972) reported estimates of Jemez Mountains salamanders ten times greater than ours, he noted that their distribution was spotty.

A better fit to a discriminant model might be obtained by including variables that we did not measure, e.g., fire and logging history and soil characteristics (moisture, pH, and compaction). Williams (1976) suggested that logging may have eliminated Jemez Mountains salamanders from part of Peralta Canyon due to dry conditions resulting from removal of most of the canopy. However, there was no documentation that salamanders occurred at the site prior to logging. Soil characteristics, which can be affected by fire and logging practices (Childs and Flint 1987, DeByle 1981, Krag et al. 1986), also can influence the distribution of plethodontid salamanders, that occupy the soil-litter interface. *Plethodon cinereus* was excluded from 27% of forest habitat in eastern deciduous forests because of low soil pH (Wyman and Hawksley-Lescault 1987), while

the distributions of up to 10 amphibians in southeastern New York were significantly influenced by soil pH and moisture (Wyman 1988).

Salamanders also may be absent from a given site for reasons other than unsuitability of habitat. For example, access to a particular area by salamanders may be impossible due to the unsuitability of the area that surrounds it, e.g., dry, open field. Or, a climatic event may have eliminated salamanders from a given area without sufficient time occurring for them to recolonize the site.

Sacramento Mountain Salamander

The variables selected by canonical analysis were able to discriminate between transects with and without salamanders. However, these variables had limited predictive value. Although a larger percentage of transects without salamanders were correctly classified by PDA, there is still a one-in-five chance of being wrong in predicting that salamanders are absent from a site. For most management decisions, this level of uncertainty will not be acceptable, and ground-truth searches will have to be made.

High elevation was the best predictor of the presence of Sacramento Mountain salamanders (table 5). Weigmann et al. (1980) also found significantly more Sacramento Mountain salamanders on transects at higher elevations. The higher elevations of the Sacramento Mountains experience greater rainfall, cooler temperatures, and lower evapotranspiration rates than the lower elevations and therefore may be more hospitable to plethodontid salamanders. The low critical thermal maximum of *Aneides* probably reflects adaptations to the low temperatures characteristic of their microhabitat (Whitford 1968) and may restrict salamanders to high elevations.

Aneides is often present where the best habitat predictors indicate they should not occur. While high-elevation, wet, north-facing slopes with a mature mixed-conifer forest do harbor *Aneides*, salamanders are also found less predictably in areas that may be drier and more exposed than the model would indicate. With the exception of elevation, the ranges of habitat variables on transects occupied by salamanders are not strikingly different from those on plots without salamanders (table 4). This overlap may be due to factors not measured, e.g., fire and logging history, and it may show an ability of salamanders to persist after habitats have been altered.

Management Guidelines

Our data show that, despite some predictive power of the habitat variables, the level of uncertainty in predicting salamander occurrence may preclude their use by the USFS. At this time, we feel the best survey technique for salamanders is ground-truth surveys in wet weather during the activity season of each species. Under proper conditions, both species are easy to find and relatively unskilled persons can be quickly trained to survey habitats. Our impression was that *Plethodon* was more difficult to survey, because it tended to retreat underground during dry periods. *Aneides*, however, can usually be found even during extended dry periods.

Our attempts to explain the absence of salamanders from a given area, i.e., potential difficulty of detecting all salamanders present, and low density or patchy distribution of populations, may overlook the possibility that absence is not solely due to unsuitable habitat. Absence does not necessarily mean avoidance, but may be due to insufficient time for the animal to recolonize an area, or inaccessibility of a suitable area due to unsuitable habitat surrounding it.

In lieu of specific recommendations, the USFS needs interim management guidelines to protect the salamanders from population declines. We suggest the following steps:

1. Salamander surveys should be made on specific sale areas as early in the planning process as possible. The USFS could maintain a team of seasonal employees for such surveys and for other activities related to endangered species.
2. To the extent possible, intensive logging operations (i.e., clearcuts, seed-tree cuts, tractor logging) should not be conducted in areas occupied by salamanders. Cable logging in winter, when the ground is frozen and the salamanders are underground, is probably the least damaging activity. In comparison, tractor logging on wet soils can compact the soil to such a degree that salamanders cannot use it.
3. Modifications of current practices, such as leaving slash where it falls or leaving as much canopy as possible, help prevent the soil surface from drying out and will probably benefit salamanders.
4. Because current timber harvest schedules will inevitably lead to younger-aged stands with few or only small downed logs, a mix of young and old logs should be maintained to ensure short-term and long-term habitat components. Old logs provide cover to *Aneides* and *Plethodon*, while younger logs are potential sources of cover in future years.

Other studies provide some evidence for negative effects of logging on amphibian populations (Bennet et al. 1980, Blymer and McGinnes 1977, Bury 1983, Gordon et al. 1962, Herrington and Larsen 1985, Pough et al. 1987, Ramotnik 1988, Staub 1986, and Williams 1976) and we suspect that intensive logging, slash removal, and burning will reduce or eliminate populations of *Plethodon neomexicanus* and *Aneides hardii*. Only intensive observations of salamander populations throughout the logging cycle will provide the information needed to make management recommendations. These studies are in progress, but may require years before definitive results are available to assess the effects of logging on *Plethodon* and *Aneides*.

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Utilization Of Abandoned Mine Drifts and Fracture Caves By Bats and Salamanders: Unique Subterranean Habitat In The Ouachita Mountains¹

David A. Saugey,² Gary A. Heidt,³ Darrell R. Heath⁴

Caves and mines play an important role in the ecology of many species, serving as permanent or temporary habitats. Culver (1986) stated, "the variety of species that depends on caves during some critical time in their life cycle, such as hibernation in bats, is impressive and usually underestimated." To this statement, we add mines.

Bear Den Caves are located in Winding Stair Mountain, LeFlore County, in southeastern Oklahoma. These four caves occur in an outcrop belt of a massive sandstone unit and were formed by a number of factors, the most important being gravitational sliding and slumpage of sandstone. These four caves have more than 365 meters of mapped passageway and represent the only known caves in the Ouachita National Forest (Puckette 1974-75).

Additional subterranean habitat was formed from 1870 to 1890, when the area extending west from Hot Springs to Mena, Arkansas was the scene of a gold, lead, silver and zinc

rush. During the period of greatest activity, 1885 to 1888, over a dozen gold mines were in operation, ranging from shallow test holes to extensive linear and L-shaped drifts extending up to 150 meters into the surrounding mountains (Harrington 1986, Hudgins 1971, U.S. Army Corps of Engineers 1980). The "gold and silver boom" effectively ended with the issuance of a report which in effect stated there were no precious metals in paying quantities to be found in the area (Branner 1888). Soon thereafter, many mines were abandoned as prospectors moved West (Harrington 1986, Hudgins 1971). Through the years, other minerals, such as manganese and mercury, have been mined from the Ouachitas resulting in the excavation of numerous additional drifts; but for a variety of reasons, most have been abandoned (Clardy and Bush 1976, Stone and Bush 1984). The legacy of these mining activities has not been riches and new-found wealth, but the creation of unusual and unique wildlife habitat.

The objectives of this study were to review, compile, and consolidate existing literature concerning utilization of caves and mine drifts by bats and salamanders in the Ouachita Mountains. In addition, we provide new data and propose recommendations concerning management of caves and mines in the Ouachita National Forest and on other public and private lands.

Abstract.—Twenty-seven abandoned mine drifts and four fracture caves constitute one of the most unique habitats in and adjacent to the Ouachita National Forest, an area devoid of solutional caves. Six species of salamanders and nine species of bats were found to utilize these areas.

METHODS

During the past six years, 27 abandoned mines in Garland (8), Montgomery (3), Pike (4) and Polk (12) counties, Arkansas (fig. 1) were located and visited a minimum of eight times (at least once each season). In several cases, where endemic or Category II (U.S. Federal Register 1985) species occurred or breeding populations were found, mines were visited much more often. Mist netting of entrances for bats was conducted in spring, summer, and fall. Bear Den Caves came to our attention during 1987 and were visited several times. Collections were minimal (mines only) and voucher speci-

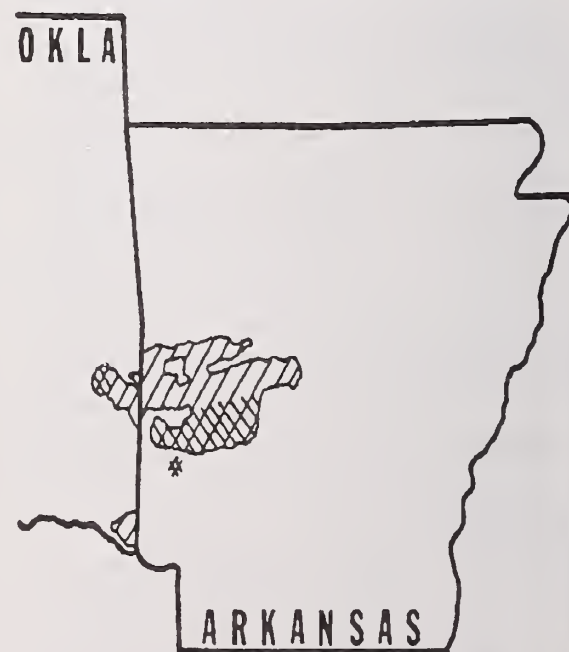


Figure 1.—Location of Ouachita National Forest (backslashed area) and study area (crosshatched area).

¹Paper presented at symposium, *Management of Amphibians, Reptiles, and Small Mammals in North America*. (Flagstaff, AZ, July 19-21, 1988).

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mens are located in the Vertebrate Collections at the University of Arkansas at Little Rock and Arkansas State University.

Following McDaniel and Smith (1976), we include the probable ecological position of the species in the cave and mine environments. This is followed by comments concerning the status or life history of each species. Following Barr (1963) and McDaniel and Smith (1976) the terms "troglophile" (commonly found in caves), "troglaxene" (may be common in caves but must leave to complete their life history), and "accidental" (unable to survive long in the cave environment) have been employed in the species accounts.

RESULTS

Nine species of bats and six species of salamanders were found to utilize caves and abandoned mine drifts during some portion of their annual cycles.

Annotated List of Bats and Salamanders Utilizing Caves and Abandoned Mine Drifts

CLASS AMPHIBIA

Order Urodela

Family Plethodontidae

Desmognathus brimleyorum (Stejneger). Troglophile.

Means (1974) stated the Ouachita dusky salamander was confined to rocky, gravelly, streams in the Ouachita Mountains. Rock falls along the upper portions of streams represented particularly good adult habitat. This species was most abundant where water percolated through rocky substrate in streambeds and along stream sides. Description of egg clutch characteristics and stream/streamside deposition were

given by Means (1974) and Trauth (1988) provided descriptions of deposition sites in seepage areas during the severe summer drought in 1980. Heath et al. (1986) reported the occurrence of this endemic salamander in four drifts, with egg clutches deposited on the underside of rocks in one mine and the presence of larvae in two others. In those mines with larvae, pools contained abundant leaf litter and isopods. On one occasion, larvae were observed feeding on isopods. Since these observations were made, numerous additional visits to these four mines revealed the presence of *Desmognathus* when epigean conditions would be considered ideal. The pools within these and other drifts are the result of seepage through walls which, in some instances, provided sufficient volumes of water to have small streams flowing from their entrances. However, unlike the preferred, gravel-bottomed stream habitat, pools typically exhibited silted substrates with very little rubble and few rocks large enough for egg attachment.

Eurycea multiplicata (Cope). Troglophile.

The many-ribbed salamander is primarily an aquatic species endemic to the Interior Highland region and adjacent areas that contain suitable habitat. It may be found under stones, logs, and other debris in clear, rock or gravel-bottomed streams (Bishop 1943, Ireland 1971, Reagan 1974). It inhabits essentially the same habitat as *Desmognathus brimleyorum* (Strecker 1908). Hurter and Strecker (1909) noted *Desmognathus* eating *Eurycea* individuals with which they were confined. Heath et al. (1986) reported both larvae and adults in two mines and in one, larvae shared the same pools with *Desmognathus* larvae. Both mines contained shallow streams with a gravel substrate. One addi-

tional mine contained larvae of this species. A seepage stream in this mine was approximately five centimeters wide, one centimeter deep, and extended a distance of sixty centimeters before dropping into a large pool at the entrance. The pool connected directly to an epigean stream.

Plethodon caddoensis Pope and Pope. Troglophile.

Large aggregations of the endemic Caddo Mountain salamander using drifts as refugia to escape heat and dryness during summer and fall were first reported by Saugey et al. (1985). Over 100 individuals were discovered in each of two drifts, from June through September 1983. Subsequent visits to these and other drifts revealed limited use of three additional drifts and use of one of the original aggregation sites for egg deposition and breeding (Heath et al. 1986). Since these observations were made, summer aggregations of this salamander have numbered as high as 383 individuals and additional egg clutches have been observed and monitored. Known only from the Novaculite Uplift area of the Ouachita Mountains in Howard, Montgomery, and Polk counties in Arkansas (Blair and Lindsey 1965, Robison and Smith 1982), this salamander and its habitat are of special concern to the Arkansas Natural Heritage Commission (ANHC) (Smith 1984). In 1985, the U.S. Fish and Wildlife Service (USFWS) designated it a Category II species. In 1986, the U.S. Forest Service (Ouachita National Forest) began informal consultation with the USFWS (Jackson, Mississippi, Endangered Species Field Station) and requested field assistance from the ANHC concerning preservation of critical mine aggregation sites and protection of their vulnerable populations. Placement of a gate at one sensitive site is planned in 1988 (fig. 2).

***Plethodon glutinosus glutinosus* (Green). Troglophile.**

The slimy salamander, a woodland species, is widely distributed, exploiting virtually every available terrestrial habitat. This species is commonly found under rocks, in and under well rotted logs and stumps, and buried deep in moist layers of leaf litter. During hotter and drier portions of the year, they usually retreat deeper into the substrate. Although primarily epigean, this salamander has been reported to use caves for aggregation sites, egg deposition and brooding, and escape from inhospitable surface environmental conditions (Barnett 1970, Noble and Marshall 1929). Heath et al. (1986) reported this salamander from five mines; two contained breeding populations and brooding behavior has been observed several times. Subsequent observations have confirmed another of the five mines as an egg deposition and brooding site. One of the mines reported with a breeding population (Heath et al. 1986) is the site of an annual aggregation of slimy salamanders exceeding 600 individuals. A gate (fig. 2) has been constructed by the U.S. Army Corps of Engineers to protect this population. Continuing studies to determine the effect of gating will allow comparison of pre- and post-gating data.

***Plethodon ouachitae* Dunn and Heinze. Troglophile.**

Endemic to the Ouachita Mountains of Arkansas and Oklahoma, the Rich Mountain salamander may be found living beneath rotting logs and stumps. However, it lives primarily under pieces of sandstone on heavily overgrown talus north slopes (Black 1974, Dunn and Heinze 1933, Pope and Pope 1951, Sievert 1986). Reagan (1974) listed this species as "endangered and vulnerable" in Arkansas. Ashton (1976) and Black (1980) both considered this salamander "threat-

ened" in Oklahoma. Sievert (1986) proposed it as a species of "special concern," conditional on his recommendations concerning silvicultural practices on National Forest lands. Black (1974) reported this salamander in Bear Den Caves where they were found throughout, but most commonly within the first 19 meters or twilight zone. A small juvenile with a snout-vent length (SVL) of < 7 mm was found in an entrance and the presence of numerous juveniles with SVLs of > 30mm may indicate egg deposition and brooding activities. One of the authors (DAS) visited these caves in December, 1987 and observed one adult Rich Mountain salamander near the entrance of one cave. An additional visit in June 1988 resulted in the observation of 30+ salamanders of various size classes. Considerable human refuse and a well worn path indicated substantial numbers of visitors. Considering the uniqueness of this area and the Category II status of this salamander, steps are being taken to exclude excessive visitation and protect this population from vandalism and overcollection. These caves are utilized by the small-footed bat, *Myotis leibii*, (Caire 1985) also a Category II species.

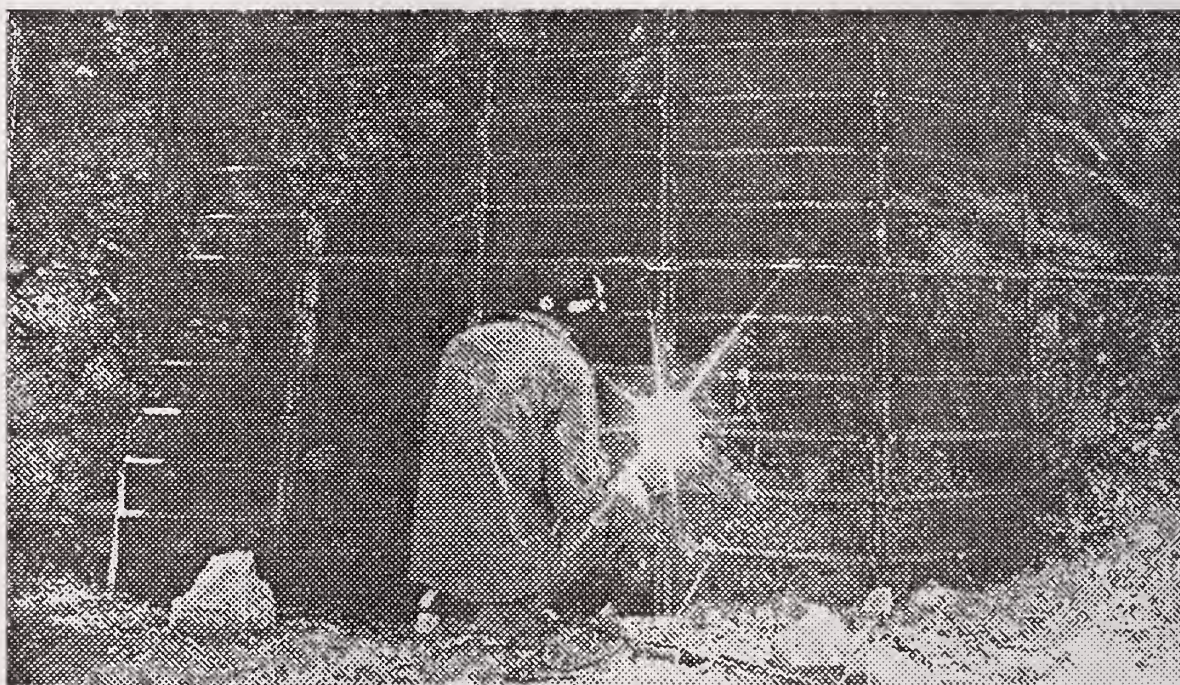


Figure 2.—Example of gate constructed by the Ouachita National Forest and the U.S. Army Corps of Engineers at the entrance of an abandoned mine (using USFWS specifications).

***Plethodon serratus* Grobman. Troglophile.**

The endemic Ouachita Red-backed salamander is commonly found beneath rocks, logs, and in leaf litter at all elevations throughout the Ouachita Mountains. This species has been observed in one mine on two separate occasions. In both cases, it has been in association with large aggregations of the Caddo Mountain salamander during extremely dry epigean conditions. Reagan (1974) frequently found this species in association with the Caddo Mountain and Rich Mountain salamanders.

CLASS MAMMALIA

Order Chiroptera

Family Vespertilionidae

***Myotis austroriparius* (Rhoads). Troglaxene.**

The first Arkansas specimens of the southeastern bat were collected from one of several drifts located 12 miles northwest of Hot Springs, Garland County, Arkansas (Davis et al. 1955).

At the time of collection (November 1952) and during a subsequent visit, this species was found in association with the little brown bat, *Myotis lucifugus*, and Keen's bat, *Myotis keenii*. This particular drift was inundated by the filling of Lake Ouachita in 1955 and, since that time, no additional specimens have been observed in nearby drifts. The second occurrence of this species in the Ouachita Mountain area was from abandoned Cinnabar mines located on an peninsula in Lake Greeson, Pike County, Arkansas (Heath et al. 1986). During a winter visit (January 1984) over 150 individuals of both red and gray color phases were observed in deep torpor. A subsequent early spring visit (March 1986), revealed 15 individuals. During December, 1986, only a few scattered individuals were found. According to personnel familiar with the drift, considerable human visitation and disturbance may have been the cause of sharp decline in use of this excavation. Mumford and Whitaker (1982) suggested the southeastern bat does not tolerate disturbance and is likely to change its roosting and hibernation sites quite readily. Caire (1985) did not report this species, but records exist for the Little River drainage in southeastern Oklahoma (Glass and Ward 1959). The southeastern bat is listed as a Category II species in the U.S. Federal Register (1985).

***Myotis keenii* (Merriam).
Trogloxene.**

Utilization of caves and mines by Keen's bat has been well documented (Barbour and Davis 1969, Heath et al. 1986, McDaniel and Gardner 1977). Sealander and Young (1955) first reported the occurrence of Keen's bat from the Ouachita Mountain area when three specimens were collected from the drift located 12 miles northwest of Hot Springs. Caire (1985) mist-netted a number of specimens at Bear Den Caves; the majority were

males with a few postlactating females. Heath et al. (1986) found this bat in 12 drifts. The largest hibernating aggregation consisted of 12 bats, including both males and females. Normally, from one to three individuals (usually males) were found hibernating in small cracks and crevices near entrances. On occasion, two have been found together in drill holes in ceilings and walls and, less frequently, individuals were observed hanging in the open. The largest non-hibernating cluster was 57 females found in the spring of 1985. Three were collected and found to be pregnant (drifts were not used as maternity roosts). Although utilized more frequently during winter months, these drifts contained from one to several Keen's bats throughout most of the year.

***Myotis leibii* (Audubon and Bachman). Trogloxene.**

The small-footed bat is very common and widespread in the western United States where it readily uses caves and mines for hibernation. In the eastern United States it is considered to be rare (Barbour and Davis 1969, Smith 1984). Caire (1985) reported mist-netting four males, three adults and one subadult, at Bear Den Caves. Specimens collected in September had descended testes. Heath et al. (1986) did not record this bat from drifts in Arkansas. According to Barbour and Davis (1969), the only known winter habitats for this species are caves and mines. Preferred hibernation sites are near entrances where temperatures drop below freezing and humidity is relatively low. Abandoned drifts in the Ouachitas generally have one, small, partially collapsed entrance which ensures relatively warm interiors (18 C) with high humidities, which is unsuitable hibernating habitat. Mist-netting of creeks and drift entrances and subsequent winter visits to drifts have been unsuccessful in locating

this bat. Caire (1985) indicated this species is probably restricted to cave areas. Thus, the few caves in southeastern Oklahoma are critical to the species survival and are in need of protection. The small-footed bat is a Category II species (U.S. Federal Register 1985).

***Myotis lucifugus* (LeConte).
Trogloxene.**

The little brown bat appears to be extremely rare in the Ouachita Mountains. It had been reported from one drift by Sealander and Young (1955), but an additional specimen was reported by Heath et al. (1986) from a drift in Arkansas. In Oklahoma, the little brown bat has been collected only from Beavers Bend State Park in the southeastern part of the state (Glass and Ward 1959).

***Myotis sodalis* Miller and Allen.
Trogloxene.**

Sealander and Young (1955) reported a misidentified Indiana bat from a now inundated drift northwest of Hot Springs. There is a confirmed record of the species from a southeastern Oklahoma cave (Glass and Ward 1959). Neither Caire (1985) nor Heath et al. (1986) found this species inhabiting mines or caves in the Ouachitas.

***Pipistrellus subflavus* (F. Cuvier).
Trogloxene.**

The eastern pipistrelle was described as fairly abundant in southeastern Oklahoma (Caire 1985) and as widespread and abundant in the Arkansas portion of the Ouachitas (Heath et al. 1986). Barbour and Davis (1969) described it as the most abundant bat over much of the eastern United States. Caves and mines appear to be important habitats for winter hiber-

nation sites and for summer night roosts (Barbour and Davis 1969, McDaniel and Gardner 1977). Caire (1985) reported capturing many individuals at Bear Den Caves during summer months. Heath et al. (1986) reported this species had been observed in every drift at all times of the year and that, over a three year period, one drift had an annual population of between 600-800 hibernating individuals. Visits to this hibernaculum over the past three years have revealed the number of individuals to be fairly constant. Preliminary observations of a drift that has had a gate in its entrance for two years have indicated an increase in numbers of hibernating pipistrelles.

***Eptesicus fuscus* (Palisot de Beauvois). Troglaxene.**

Heath et al. (1986) reported that, although common in the Ouachita Mountain area, the big brown bat was rarely found hibernating in drifts. The four drifts used during hibernation had larger, less restricted, openings that created a variable temperature zone. Rarely were more than two or three observed in any drift. This species characteristically chose hibernating sites near the entrance where temperature and humidity levels were lower. Similar hibernating behavior has been documented in other caves and mines (Barbour and Davis 1969, Lacki and Bookhout 1983). Caire (1985) reported this species from Bear Den Caves.

***Lasionycteris noctivagans* (LeConte). Troglaxene.**

Typically considered a tree bat, the silver-haired bat has been found in numerous caves and mines (Barbour and Davis 1969, Saugey et al. 1978, Whitaker and Winter 1977). Heath et al. (1986) discovered a single specimen hibernating in a breezeway of a

drift near Lake Greeson; the ambient temperature was 2 C.

The three following species of *Lasiurus*, normally considered tree bats, have been captured during swarming activities at the entrances of, but not inside drifts (Heath et al. 1983, 1986). Similar behavior in tree bats has been observed at caves (Barbour and Davis 1969, Harvey et al. 1981).

***Lasiurus borealis* (Muller).
Accidental.**

The red bat was captured at the entrances of three drifts. Caire (1985) reported capturing this species at Bear Den Caves. Red bats were reported from inside two Ozark caves by McDaniel and Gardner (1977). Saugey et al. (1978) discovered the remains of 140 red bats in one Ozark cave.

***Lasiurus seminolus* (Rhoads).
Accidental.**

Heath et al. (1983) reported the capture of a female Seminole bat at the entrance to a drift in Polk County, Arkansas, during September.

***Lasiurus cinereus* (Palisot de Beauvois). Accidental.**

Previously unreported, a male hoary bat was captured simultaneously with the above mentioned Seminole bat. The occurrence of this species in mines and caves has been well documented (Barbour and Davis 1969, Saugey et al. 1978).

DISCUSSION

Caves are common and widely distributed in the United States. Caves are known in every state and, in some, are very common. It has been found that most caves contain a biologically interesting fauna (Culver

1986). Where caves are scarce, abandoned mineshafts occasionally provide the same specialized habitat as do natural caves (Barbour and Davis 1969).

Abandoned mine drifts and fracture caves represent important habitat features in the Ouachita Mountains. Six species of salamanders and nine species of bats utilize these structures for some purpose. In addition, four of the six salamanders are endemic to the Ouachita Mountains, and a fifth is endemic to the Interior Highlands. Two of these salamanders, *Plethodon caddoensis* and *P. ouachitae*, are Category II species. For all of these salamanders, caves and mines may only represent larger versions of existing subterranean microhabitats, complimenting existing situations and not replacing them. However, caves and mines do provide "natural laboratories" where insights into life histories and species interactions, otherwise unobservable, may be studied with the knowledge gained applied to management of surface populations.

Six of the nine species of bats regularly frequent caves or mines during some portion of their annual cycles and two of these are listed as Category II species (*Myotis austroriparius* and *M. leibii*). Mines provide a key habitat component for bats where natural subterranean hibernacula are scarce. Hibernacula can be viewed as islands of different sizes and complexities in an ocean of habitat inhospitable for hibernation (Gates et al. 1984). Most caves and mines in the Ouachitas are small and marginal as hibernacula when compared with extensive and complex cave systems of other regions. However, minor hibernacula may become major ones (depending on their size, configuration, and microclimate), if the latter are destroyed. Further, they may function to promote range expansions (Gates et al. 1984). In addition, small populations become increasingly important in species management when large populations are

continually threatened (Humphrey 1978).

Fifty-three vertebrate taxa use Ozark caves (McDaniel and Gardner 1977). Heath et al. (1986) reported the occurrence of 27 vertebrate taxa utilizing abandoned mine drifts in the Ouachita Mountains. Caire (1985) and Black (1974) reported two species from Bear Den Caves. We report two additional species from abandoned mines (*Lasiurus cinereus* and *Plethodon serratus*). Of the 31 recorded species that use caves and mines in the Ouachita Mountains, 22 are common to both the Ouachitas and Ozarks.

These data further support Maser et al (1979) when they stated, "Unique habitats occupy a very small percent of the total forest land base, yet they are disproportionately important as wildlife habitats." From our measurement, the total area of all known and inventoried caves and drifts in the Ouachita Mountains is approximately one acre in a forest with nearly 1.6 million surface acres. For these reasons, resource managers should not overlook opportunities to protect and conserve what may appear to be marginal sites, especially in areas where these unique habitats may be a limiting factor.

MANAGEMENT RECOMMENDATIONS

While the National Forest Management Act (1976) and Endangered Species Act (1973) specify objectives and set policy, the Forest Service Manual provides guidance and direction to realize these objectives relating to species of special concern and their habitats. These documents mandate consideration of these unique and valuable resources in all phases of planning and project implementation.

Nieland and Thornton (1985), Nieland (1985), Hathorn and Thornton (1986), and Chaney (1984) provide additional information, guidance and

considerations concerning management, inventory and evaluation of caves. Caire (1985) made recommendations about habitat management for bats, including Bear Den Caves in southeastern Oklahoma, and Sievert (1986) proposed guidelines for preservation of habitat for the endemic Rich Mountain salamander.

Because management of cave resources are adequately addressed in these references, the following recommendations address issues concerning needed management of abandoned mine drifts whose importance to bats and other vertebrates has been demonstrated by Heath et al. (1986), Lacki and Bookhout (1983), Saugey et al. (1985), Whitaker and Winter (1977) and this study.

In line with these studies, we recommend the following actions be taken on National Forests, other public lands, and private lands:

1. Address abandoned mine drifts and shafts as "unique subterranean habitat" in the Cave Management section of the Forest Service Manual. Most of the language in this chapter is directly applicable to these excavations.
2. Incorporate management prescriptions for abandoned mine drifts into Forest Land Management Plans and other resource management planning documents, where applicable.
3. Develop specific supplements, for individual National Forests, to the Forest Service Manual concerning the inventory, evaluation, and management of these excavations.
4. Prepare a chapter in the Ouachita National Forest Wildlife Handbook providing direction and guidance concerning management of

abandoned mine drifts and coordination with other resources.

5. Use full seasonal or partial closures to protect species of special concern during critical periods of the year.
6. Acquire lands within agency administrative authority that contain caves and abandoned mine drifts.
7. Prohibit extraction of minerals and other materials from abandoned mine drifts.
8. Identify and designate abandoned mine drifts, caves, and associated above ground habitat as "key areas" for wildlife during the silvicultural prescription process.
9. Set aside and preserve travel corridors to prevent isolation and loss of use by terrestrial vertebrates.
10. Establish monitoring activities to assess changes in the drift environment and associated wildlife utilization.
11. Continue inventory of species utilizing drifts and determine how and what they are using them for.
12. Cooperate, consult, and coordinate with state and federal resource management agencies, universities and colleges, public and private conservation organizations, and other interested publics to promote conservation, education, and research.

"Ultimately, the survival of most animal species depends more on habitat protection than on direct shielding of the creatures themselves" (Smith 1984).

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The Herpetofauna of Long Pine Key, Everglades National Park, in Relation to Vegetation and Hydrology¹

George H. Dalrymple²

Many authors have noted a general reduction in species diversity among animal groups as latitude decreases in peninsular Florida (Dinnen 1984, Loftus and Kushlan 1987, for fishes; Duellman and Schwartz 1958, Kiestner 1971, for amphibians and reptiles; Cook 1969, Robertson and Kushlan 1984, for birds; Simpson 1964, Layne 1984, for mammals). Simpson (1964) considered such a "peninsular effect" to be due to a greater rate of extinction and, or a lower rate of immigration along peninsulas in comparison to the mainland.

Species area curves (Preston 1962, MacArthur and Wilson 1967) for lizards and snakes evaluated by Busack and Hedges (1984) showed that there was no significant peninsular effect in Florida. There was, however, a general trend for reduced species numbers as one proceeds down the peninsula of Florida, most likely caused by a reduction in habitat quality. Moreover, Robertson's (1955) study of breeding land birds of the Long Pine Key region of Everglades National Park, the southern most Upland region on the mainland, revealed both lower species richness and lower densities within species

than in other areas. This reduced abundance of animals agrees with the general belief that productivity is low in southern Florida Pinelands (oligotrophic, Snyder 1986). When Duellman and Schwartz (1958) described the southern Florida herpetofauna as "depauperate...for a warm lowland area" they were referring to the lower number of species (table 1). It has remained unclear whether characterization of the herpetofauna as depauperate applies to all habitat types in the region, in-

cludes both low species and population numbers and applies to all taxa.

The main objectives of this study are to:

1. develop a species list of amphibians and reptiles in Long Pine Key-Paradise Key area (abbreviated LPK herein),
2. describe species associations with vegetation characteristics,

Table 1.—The number of species of amphibians and reptiles found in Florida, southern Florida and in Long Pine Key¹

Taxa	Florida	Southern Florida		Long Pine Key	
	#	#	(%)	#	(%)
Salamanders	24	4	(17)	3	(13)
Frogs and toads	29	16	(55)	12	(41)
Amphibian					
Subtotal	53	20	(38)	15	(28)
Turtles	20	11	(55)	8	(40)
Crocodilians	2	2	(100)	1	(50)
Lizards	16	11	(69)	6	(38)
Snakes	41	28	(68)	21	(52)
Reptile					
Subtotal	79	52	(66)	36	(46)
Totals	132	72	(55)	51	(39)

¹The data for Florida and southern Florida are based upon current species lists (Wilson and Porras, 1983; Auffenberg, 1982). The numbers for Long Pine Key are for the current study (see text). Since Long Pine Key column includes the exotic species *Eleutherodactylus planirostris*, *Osteopilus septentrionalis* and *Anolis sagrei* they have been included in the counts for the first two columns also. (Salamander list includes *Stereochilus marginatus*; frog list includes the new species *Rana okaloosae* (Moler, 1985).

¹Paper presented at symposium, Management of Amphibians, Reptiles, and Small Mammals in North America. (Flagstaff, AZ, July 19-21, 1988.)

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3. evaluate correlations between species' phenologies and rainfall patterns in the area,
4. estimate abundances of species and compare them to other areas in North America.

Study Area

The Long Pine Key (LPK) region was chosen for study because this 8000 ha area is the principal remaining natural upland region of the original Miami (or Atlantic) Rock Ridge physiographic province (Davis 1943) and as part of Everglades National Park it has been protected from human interference for nearly 40 years. The region includes about 4650 ha of Pinelands (Snyder 1986) with a series of "transverse or finger glades," or

seasonally flooded Prairies, interspersed throughout the Pinelands (fig. 1). Within the Pinelands there is a series of at least 120 tropical hardwood Hammocks (Olmsted et al. 1983, fig. 2) varying in size from .1 ha to 91 ha (Olmsted, Loope and Hilsenbeck 1980). Most Hammocks are completely surrounded by Pineland and are kept rather small due to the frequent fires (prescribed burns and natural fires from lightning) in the region. The largest Hammock, Royal Palm, is surrounded by seasonally flooded Prairies and has almost completely overgrown the limestone elevation known as Paradise Key (these names are sometimes used interchangeably). Because Paradise Key figured importantly in the study of Duellman and Schwartz (1958), I have included it in the present study as part of the general area described herein as LPK.

On the southern border of LPK

about 3600 ha of land were farmed until 1975 (abandonment was an attenuated process from the 1960's to 1975), when this agricultural area, known as the "hole-in-the donut," was purchased by the Park Service. Early farming was limited to areas with deeper soil, and involved little alteration of the underlying bedrock. Starting in 1954 (W.B. Robertson, Jr. pers. comm.) rock-plowing of the upper 20 cm of the ground surface created an artificial soil: "deeper, better drained, better aerated, and possibly more nutrient-rich than the pre-farming soil" on 1600 of the 3600 ha (Ewel et al. 1982:1-2). The substrate alteration proved conducive to the establishment of exotic vegetation, especially Brazilian Pepper (*Schinus terebinthifolius*) after the farmland was abandoned (Ewel et al. 1982).

Existing detailed surveys of the region's vegetation in relation to elevation, fire and hydrology (e.g. Olmsted et al 1980; Olmsted et al. 1983; Olmsted and Loope 1984; Taylor and Herndon 1981) as well as an extremely detailed vegetation map of the area (Johnson et al. 1983) have made it much easier to plan the current project. Historical surveys of the literature in the above cited references, among many others, make it clear that the LPK region has not been completely free from disturbances: logging of the Pinelands during the 1930's and 1940's; farming, as described above; invasion by exotic vegetation; development of elevated roadways with marl dug from local pits and their resulting small canals, culverts and ponds bordering the former farmlands (all of which distort the original associations of elevation, soil, vegetation and surface water); fire roads, to help control prescribed burns; and the inevitable presence of humans and their buildings (both those for visitors and the complex of staff facilities). All of these factors play a role in determining the present herpetofauna. Current park management fosters a de-



Figure 1.—Aerial photograph of Pineland and Prairie of Long Pine Key.

large enough to ensure lasting preservation of this unique ecosystem type.

Materials and Methods

General Collecting and Road Cruising

For the 3 years of the study reported on herein many hours were spent surveying and trapping in areas for evidence of amphibians and reptiles. Each time the traps were checked, a 50 km section of unimproved dirt roads was driven over by van, and an additional 15 km paved road was systematically covered by van for a total of 8 to 16 hours per week, during which all animals were captured and identified. Searches on foot, by teams of two to four people, were conducted in all of the major habitats each week, during which animals were searched for at the surface and under rocks and logs. The time spent collecting and road cruising was divided between day and night to ensure that all species in LPK might be found.

Trapping

I used a system of funnel traps attached to drift fences and transects (referred to throughout as "arrays"). Many researchers have used arrays to study amphibians and reptiles (Campbell and Christman 1982b, Clawson and Baskett 1982, Vogt and Hine 1982, Gibbons and Semlitsch 1981, Clark 1970), however they all employed arrays that included both funnel traps and pit traps. Usually the pit traps are placed at regular intervals by digging holes in the ground. However, the lack of well developed soils coupled with an irregular limestone surface made the use of pit traps impractical to use in the everglades.

Each array was constructed of four fifteen meter long sheets of shade cloth (one meter tall) that

intersected in the middle to form an "x." The shade cloth was kept upright by tying it to iron rebar that were hammered into the limestone. Traps were made of cylinders of one-eighth inch hardware cloth approximately 1 m in length and 30 cm in diameter. Each trap was fitted with two funnels (one funnel on each side of the shade cloth fencing) made of the same material. Funnels were attached to the free ends of the four arms of the array. Shade cloth had 12-cm flaps sewn onto the bottom edge to conform to the irregular surfaces of the everglades terrain. Flaps were covered with natural soils and or leaf litter so that animals would not crawl under them (figs. 3 and 4). The square area encompassed by each array was .10 ha.

Arrays were placed in each of four main habitat types: seasonally flooded Prairies, Pinelands, tropical

hardwood Hammocks, and in the area of secondary succession from former farming, the "hole-in-the-donut." The latter area is referred to throughout as "Disturbed." Thirteen arrays were maintained starting in May, 1984, and the arrays are still checked to the current date. Three arrays were placed in each habitat type within Long Pine Key and one extra hammock array was maintained in Royal Palm Hammock on Paradise Key (fig. 5). Arrays were temporarily taken down during park service prescribed burns and replaced after the burns. Because arrays were in place for different durations, I assessed yield in terms of rate of capture, rather than absolute capture yield, and capture rate was assessed separately for wet and dry seasons. At each array we maintained two 1-m² pieces of tar-paper, under which we commonly collected



Figure 2.—Aerial photograph of Pineland and Hammocks in Long Pine Key.



Figure 3.—Aerial photograph of locality known as New Wave Prairie in Long Pine Key with "x"-shaped trapping array visible at left (each of the four arms of the array is 15 m long).



Figure 4.—Ground level view of trapping array fencing in Pineland.

seasons. At each array we maintained two 1-m² pieces of tar-paper, under which we commonly collected animals. All animals caught along the fences or under the tar paper at an array were counted as part of the capture rate at the array in question.

Symbolic Star Plot Analysis

Symbolic Star Plot Analysis (Chambers et al. 1983) was chosen as a useful multivariate method for graphically depicting the rates of capture of species in the major habitats. Only species for which there were at least ten captures were chosen, and the analyses were based on the number of animals trapped per 1000 array days because the raw data does not reflect the fact that arrays were operational for varying time periods. The data values are used as the lengths of the rays of the stars for each habitat. All data values were rescaled to range from 1 to c , where c is the length of the smallest ray (set to 0.1 for these analyses). According to Chambers et al. (1983:158): "If x_{ij} is the j^{th} measurement of the i^{th} variable then the scaled variable $[x^*_{ij}]$ is

$$x^*_{ij} = (1 - c)(x_{ij} - \min x_{ij}) / (\max x_{ij} - \min x_{ij}) + c."$$

The scaled variables are arranged around a circle at equal angles, the number of angles determined by the number of variables, and the actual rays are drawn by connecting points trigonometrically calculated for an arbitrarily chosen maximum radius for the circle.

The lengths of the rays (not the area adjoining the rays) in the four habitat stars for a given species represent the proportion of all captures for that species in each habitat. The result is intended to form a simple yet "dramatic and memorable" impression of the relationships within species and between habitat types, for further details see Chambers et al. (1983:158-163).

Population Abundance Estimates

For most species the actual numbers presented are actual numbers of individuals captured. All snakes and turtles were individually marked. The anurans and lizards were marked only during 1984, but due to the lack of recaptures I stopped marking in 1985. The marking method used for snakes was that of Brown and Parker (1976), and even though snakes were marked for four consecutive years (1984-1987) the recapture rate remained very low (<0.05 , Dalrymple, in prep.).

Concentrations of amphibians and reptiles around one or more resources, such as water (ponds or lakes, Carpenter 1952, Reichenbach and Dalrymple 1986), hibernacula (caves, pits and dens, Woodbury 1951, Brown and Parker 1982a, Aleksuk and Gregory 1974) breeding sites (Crump 1982, Brown and Parker 1982b, Wiest 1982) and or food (Hamilton 1951) lead to recaptures that allow for density estimates with confidence limits (cf. Turner 1971). These estimates are dependent on seasonal fluctuations, and may differ greatly from estimates of crude density. However, few concentrations were found on LPK particularly because water was readily available in numerous solution holes in every habitat. Moreover, mild winters allowed most species to be active throughout the year, and the ability of animals to readily go underground through the porous limestone and plentiful solution holes found in all habitats resulted in the absence of group hibernacula. Further complicating density estimation were widespread movements in search of mates, and the fact that major food sources were not clumped.

All these factors lead to a wide spread distribution of most species in the region and most were not habitat specialists, at least at the major vegetation type level. The lack of concentrations and the limited number of recaptures permit only the presenta-

tion of total numbers of captures and not accurate density estimates at this time.

Results

Species List

Starting in January, 1984, 51 species of amphibians and reptiles were observed or collected in LPK (table 2). Some species were rare because they are most commonly associated with more permanently aquatic habitats, such as the Sloughs (e.g. *Acris gryllus*, *Rana grylio*, *Trionyx ferox*, *Farancia abacura*, *Nerodia cyclopion*, *Nerodia taxipilota*, *Regina alleni*). A few species

that have been recorded in the larger geographic region were not found in LPK during this study (*Scaphiopus holbrooki*, *Pseudobranchius striatus*, *Seminatrix pygaea*, *Masticophis flagellum*, *Heterodon platyrhinos*, *Ophisaurus ventralis*, *Sternotherus odoratus*).

Trapping Results

Between May, 1984 and December, 1986, 1709 amphibians and reptiles were collected either in the traps, under associated tar paper, or along array fences (table 3). These animals represent 37 of the 51 species (73%) known from our overall surveys. I compared the four habitats by recording the number of animals per

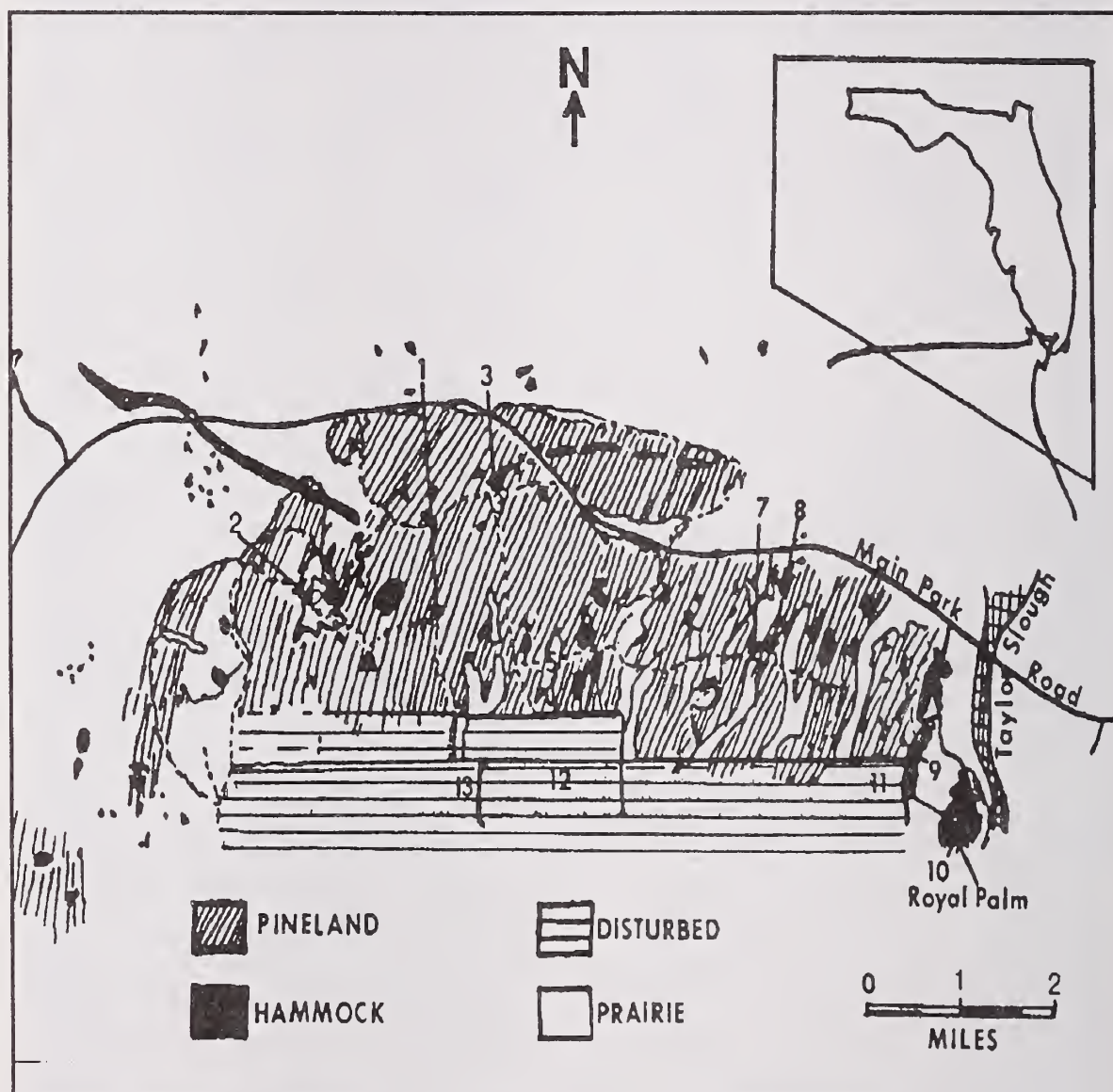


Figure 5.—Map of the Long Pine Key-Paradise Key region of Everglades National Park. Array locations are numbered and referred to in the text as follows: 1. Pine Block B, 2. New Wave Prairie, 3. Pine Block E, 4. Junk Hammock, 5. Serenoa Prairie, 6. Wright Hammock, 7. Mud Prairie, 8. Pine Block H, 9. Palma Vista I Hammock, 10. Royal Palm Hammock, 11. Burnout Disturbed, 12. Schinus Disturbed, 13. Grass Disturbed.

Table 2.—List of species of amphibians and reptiles observed in the Long Pine Key - Paradise Key region of Everglades National Park during present study, between January, 1984 and December, 1986. The regionwide natural habitat associations of Duellman and Schwartz (1958), as they apply in the study area, are given after the scientific name for each species. Pr = Prairie, Pi = Pine, H = Hammock, A= Permanently Aquatic, i.e. Slough, Canals.

Scientific name	Common name	Scientific name	Common name
Urodela		Squamata, Lacertilia	
<i>Amphiuma means</i> -Pr A	two-toed amphiuma	<i>Anolis carolinensis</i> -Pr Pi H	green anole
<i>Siren lacertina</i> -Pr A	greater siren	<i>Anolis sagrei</i> -Pi	brown anole
<i>Notophthalmus viridescens</i> -Pr A	peninsula newt	<i>Eumeces inexpectatus</i> -Pr Pi H	southeastern five-lined skink
Anura		<i>Ophisaurus compressus</i> -Pr Pi	island glass lizard
<i>Acris gryllus</i> -Pr	Florida cricket frog	<i>Scincella laterale</i> -Pi	ground skink
<i>Bufo quercicus</i> -Pr Pi H	oak toad	<i>Sphaerodactylus notatus</i> -Pi	reef gecko
<i>Bufo terrestris</i> -Pr Pi H	southern toad	Squamata, Serpentes	
<i>Eleutherodactylus planirostris</i> -Pi	greenhouse frog	<i>Agkistrodon piscivorus</i> -Pr A	cottonmouth
<i>Gastrophryne carolinensis</i> -Pr Pi H	eastern narrow-mouthed toad	<i>Cemophora coccinea</i> -Pi	scarlet snake
<i>Hyla cinerea</i> -Pr Pi H	green treefrog	<i>Coluber constrictor</i> -Pr Pi H	black racer
<i>Hyla squirella</i> -Pr Pi H	squirrel treefrog	<i>Crotalus adamanteus</i> -Pi	eastern diamond-back
<i>Limnaeodactylus ocellatus</i> -Pr	little grass frog	<i>Diadophis punctatus</i> -Pr Pi H	ringnecked snake
<i>Osteopilus septentrionalis</i> -H *	Cuban treefrog	<i>Drymarchon corais</i> -Pr Pi H	indigo snake
<i>Pseudacris nigrita</i> -Pr Pi	Florida chorus frog	<i>Elaphe guttata</i> -Pr Pi H	corn snake
<i>Rana grylio</i> -Pr A	pig frog	<i>Elaphe obsoleta</i> -Pr Pi H	yellow rat snake
<i>Rana sphenoccephala</i> -Pr A	southern leopard frog	<i>Farancia abacura</i> -Pr A	mud snake
Testudines		<i>Lampropeltis getulus</i> -Pr Pi H	kingsnake
<i>Chelydra serpentina</i> -Pr A	snapping turtle	<i>Lampropeltis triangulum</i> -Pi	scarlet kingsnake
<i>Chrysemys floridana</i> -Pr A	peninsula cooter	<i>Micrurus fulvius</i> -Pi	coral snake
<i>Chrysemys nelsoni</i> -Pr A	red-bellied turtle	<i>Nerodia fasciata</i> -Pr A	banded water snake
<i>Deirochelys reticularia</i> -A	chicken turtle	<i>Nerodia cyclopion</i> -Pr A	green water snake
<i>Gopherus polyphemus</i> -Pi	gopher tortoise	<i>Nerodia taxispilota</i> -A	brown water snake
<i>Kinosternon bauri</i> -Pr A	striped mud turtle	<i>Opheodrys aestivus</i> -Pr Pi H	rough green snake
<i>Terrapene carolina</i> -Pr Pi H	box turtle	<i>Regina alleni</i> -Pr	striped crayfish snake
<i>Trionyx ferox</i> -A	Florida soft-shelled turtle	<i>Sistrurus miliarius</i> -Pr Pi	pigmy rattlesnake
Crocodylia		<i>Storeria dekayi</i> -Pr Pi H	brown snake
<i>Alligator mississippiensis</i> -Pr A	American alligator	<i>Thamnophis sauritus</i> -Pr Pi H	ribbon snake
		<i>Thamnophis sirtalis</i> -Pr Pi H	garter snake

array day. The highest capture rates were in seasonally flooded Prairie, which had both the most individuals and the most species collected, followed by Disturbed areas, Hammock and Pineland (table 3).

Monthly total rainfall for LPK and maximum water level from well station NP-72 in the same area for data from 1984-1986 were provided from hydrological stations maintained by the South Florida Research Center,

Everglades National Park. These data were correlated with the monthly values for animals trapped per check day. There were significant correlations between number of animals caught per check day and both monthly rainfall ($r = 0.55$, $p = .001$), and monthly maximum water levels ($r = 0.50$, $p = .004$) for the three year period (fig. 6). Rates of capture were significantly greater during the wet season than the dry season (table 4;

Wilcoxin matched pairs test, $T = 3.0$, $p < .005$). Differences in overall capture rates between the dry and wet seasons is greater in Hammock and Disturbed areas than in the Pinelands and Prairie.

Relative Abundance

Although 37 species were found at arrays they were not all equally com-

Table 3.—Total numbers of amphibians and reptiles trapped, May 1984-Dec 1986. "Check days" are number of days on which traps were checked. "Array days" are number of total days arrays were standing. Numbers in parentheses are animals per 1000 array days. Acronyms at right of table are for species used in figures 7-9.

Taxa	Prairie		Pineland		Hammock		Disturbed		Total	
<i>A. means</i>	9	(3.5)	0	(0)	0	(0)	0	(0)	9	
<i>A. gryllus</i>	1	(0.4)	0	(0)	0	(0)	0	(0)	1	
<i>B. quercicus</i>	95	(37.2)	7	(2.8)	3	(0.9)	9	(6.2)	114	Bq
<i>B. terrestris</i>	45	(17.6)	24	(9.4)	50	(15.5)	31	(21.3)	150	Bt
<i>E. planirostris</i>	15	(5.9)	17	(6.7)	50	(15.5)	6	(4.1)	88	Ep
<i>G. carolinensis</i>	10	(3.9)	1	(0.4)	21	(6.5)	33	(22.6)	65	Gc
<i>H. cinerea</i>	20	(7.8)	1	(0.4)	7	(2.2)	3	(2.1)	31	Hc
<i>H. squirella</i>	32	(12.5)	3	(1.2)	6	(1.9)	4	(2.7)	45	Hs
<i>O. septentrionalis</i>	2	(0.8)	1	(0.4)	3	(0.9)	6	(4.1)	12	Os
<i>P. nigrita</i>	5	(2.0)	8	(3.1)	0	(0)	0	(0)	13	Pn
<i>R. grylio</i>	5	(2.0)	0	(0)	0	(0)	0	(0)	5	
<i>R. sphenoccephala</i>	135	(52.8)	10	(3.9)	106	(32.8)	20	(13.7)	271	Rs
<i>A. carolinensis</i>	170	(66.5)	136	(52.3)	19	(5.9)	19	(13.0)	344	Ac
<i>A. sagrei</i>	0	(0)	0	(0)	50	(15.5)	103	(70.7)	153	As
<i>E. inexpectatus</i>	23	(9.0)	21	(8.2)	42	(13.0)	3	(2.1)	89	Ei
<i>O. compressus</i>	1	(0.4)	1	(0.4)	0	(0)	1	(0.4)	3	
<i>S. laterale</i>	30	(11.7)	9	(3.5)	3	(0.9)	0	(0)	42	Sl
<i>S. notatus</i>	0	(0)	0	(0)	29	(9.0)	0	(0)	29	Sn
<i>K. bauri</i>	12	(4.7)	2	(0.8)	1	(0.3)	1	(0.7)	16	Kb
<i>T. carolina</i>	11	(4.3)	1	(0.4)	2	(0.6)	3	(2.1)	17	Tc
<i>A. piscivorus</i>	1	(0.4)	0	(0)	0	(0)	2	(1.4)	3	
<i>C. coccinea</i>	2	(0.8)	0	(0)	0	(0)	0	(0)	2	
<i>C. constrictor</i>	8	(3.1)	30	(11.8)	14	(4.3)	14	(9.6)	66	Cc
<i>C. adamanteus</i>	0	(0)	0	(0)	0	(0)	1	(0.7)	1	
<i>D. punctatus</i>	3	(1.0)	3	(1.0)	13	(4.0)	0	(0)	19	Dp
<i>D. corais</i>	1	(0.4)	2	(0.8)	2	(0.6)	0	(0)	5	
<i>E. guttata</i>	0	(0)	1	(0.4)	0	(0)	0	(0)	1	
<i>E. obsoleta</i>	0	(0)	0	(0)	4	(1.2)	1	(0.7)	5	
<i>L. getulus</i>	0	(0)	0	(0)	0	(0)	1	(0.7)	1	
<i>L. triangulum</i>	1	(0.4)	0	(0)	0	(0)	0	(0)	1	
<i>M. fulvus</i>	0	(0)	0	(0)	4	(1.2)	0	(0)	4	
<i>N. fasciata</i>	3	(1.2)	0	(0)	0	(0)	0	(0)	3	
<i>R. alleni</i>	1	(0.4)	0	(0)	0	(0)	0	(0)	1	
<i>S. miliarius</i>	14	(5.5)	8	(3.1)	3	(0.9)	6	(4.1)	31	Sm
<i>S. dekayi</i>	2	(0.8)	0	(0)	4	(1.2)	0	(0)	6	
<i>T. sauritus</i>	8	(3.1)	1	(0.4)	10	(3.1)	0	(0)	19	Tsa
<i>T. sirtalis</i>	30	(11.7)	5	(2.0)	2	(0.6)	7	(4.8)	44	Tsi
Totals	695		292		448		274		1709	
No. Check days	669		663		789		361		2482	
Anls/Check day	1.04		0.44		0.57		0.76		0.70	
No. Species	30		22		24		21		37	
No. Array days	2555		2550		3229		1458		9792	
Anls/Array day	0.27		0.12		0.14		0.19		0.18	

mon. The most common species were anurans and lizards (table 3): *Rana sphenoccephala*, *Bufo terrestris*, and *Anolis carolinensis*. Of the 20 species of snakes collected during the study, 17 were trapped but only five were cap-

tured in high enough frequency to allow for more detailed study (*Coluber constrictor*, *Thamnophis sirtalis*, *Sistrurus miliarius*, *Diadophis punctatus*, and *Thamnophis sauritus*). As a preliminary method, abundance can

be minimally estimated as the actual counts from the "Total" column of table 3 as the number per hectare (12 arrays, each one covering approximately one-tenth of a hectare makes this a conservative estimate).

Habitat Use And Preference

A species' likelihood of being trapped is more a function of the number of individuals in the vicinity of an array than a result of any dif-

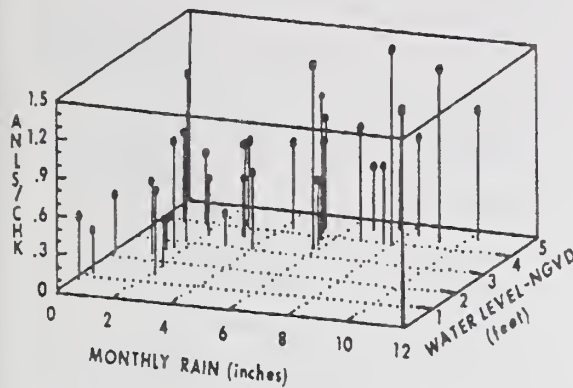


Figure 6.—Comparison of number of animals trapped per check day per month with monthly rainfall and water table values from study area between May 1984 and December 1986.

ference in trap functioning between habitats. For species with high capture rates, there were significant differences in habitat use for: *Coluber constrictor*, more common in Pine-lands (chi square = 14.59, $p = .0007$); *Thamnophis sirtalis*, *Sistrurus miliarius*, *Scincella laterale* and *Bufo quercicus* all more common in Prairie (chi squares of 42.9, 9.6, 26.4, 71.8 respectively, all with p 's $< .01$); while *Bufo terrestris* is equally common in all habitats (chi square = 2.36, $p = .51$). In most cases, species were found in more than one and usually three habitats (cf. Duellman and Schwartz 1958). Among trapped species, 41% were found in all four habitat types, 27% in two or three, and 32% in only one habitat type. Seven of the 13 species from only 1 habitat type were from Prairie.

Table 4.—Results of 1985 trapping of all individuals of amphibians and reptiles at 13 array sites organized by vegetation type, and season (dry = November-April; wet = May-October). "Check-days" are the number of days on which an array was checked for animals. Note that there is no data for the wet season for "Grass" array (see Materials and Methods). Variation within habitat types is as great as between habitat types.

Habitat/array	No. Individuals		No. species		No. check-days		Animals per check day	
Season:	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Prairie								
New Wave	65	118	12	20	54	54	1.2	2.2
Mud	38	64	10	18	56	54	0.7	1.2
Serenoa	12	20	2	10	50	51	0.2	0.4
Pineland								
Pine Block B	26	23	8	8	50	53	0.5	0.4
Pine Block H	25	39	8	11	56	51	0.5	0.8
Pine Block E	16	17	4	8	51	52	0.3	0.3
Hammocks								
Royal Palm	18	110	7	17	56	28	0.3	3.9
Palma Vista I	11	50	6	12	56	33	0.2	1.5
Wright	15	21	6	8	52	53	0.3	0.4
Junk	17	23	7	7	53	52	0.3	0.4
Disturbed								
Schinus	11	76	6	12	55	33	0.2	2.3
Burnout	11	16	6	7	45	17	0.2	0.9
Grass	14	—	4	—	18	—	0.7	—

Symbolic star plot analyses (Chambers et al. 1983) were applied to the 1984-1986 trap data for the number of animals per 1000 array days as the data set (table 3), for the anurans (fig. 7), lizards and turtles (fig. 8), and snakes (fig. 9). Since the qualitative general habitat associations of Duellman and Schwartz (1958) were corroborated in this study, I restricted this quantitative analysis to those species for which there were at least 10 captures.

It is obvious from the anuran plot that the majority of individuals and species are most prevalent in Prairie. *Pseudacris nigrita* is strongly represented in Pineland, as was noted by Duellman and Schwartz 1958). In Hammocks, *Eleutherodactylus planirostris*, *Bufo terrestris*, *Gastrophryne carolinensis*, and *Hyla cinerea* were dominant. *Rana sphenoccephala* was most common in Prairie but was very abundant in two Hammocks that are adjacent to wet Prairie and that retained water in solution holes throughout most of the year (Royal Palm and Palma Vista I). *Bufo terrestris*, *G. carolinensis* and the exotic Cuban tree frog, *Osteopilus septentrionalis*, were dominant in Disturbed habitat (fig. 7).

For the trap data for turtles, *Kinosternon bauri* and *Terrapene carolina*, and the lizards, Prairie again had the greatest abundance; but *T. carolina* was commonly found in the Disturbed habitat. *Anolis carolinensis* was well represented in Pineland and Prairie, as were the skinks, *Eumeces inexpectatus* and *Scincella laterale*. *Anolis sagrei* was restricted to Disturbed sites and Hammocks, especially those close to roads and parking lots. *Sphaerodactylus notatus* is most often found in leaf litter of Hammocks, and *E. inexpectatus* is also well represented in Hammocks (fig. 8).

For snakes, the star diagram analysis was restricted to the five most common species; again the greatest diversity and abundance is found in Prairie. *Coluber constrictor* was clearly the dominant snake in

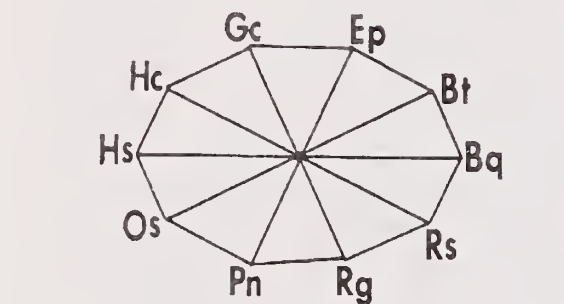
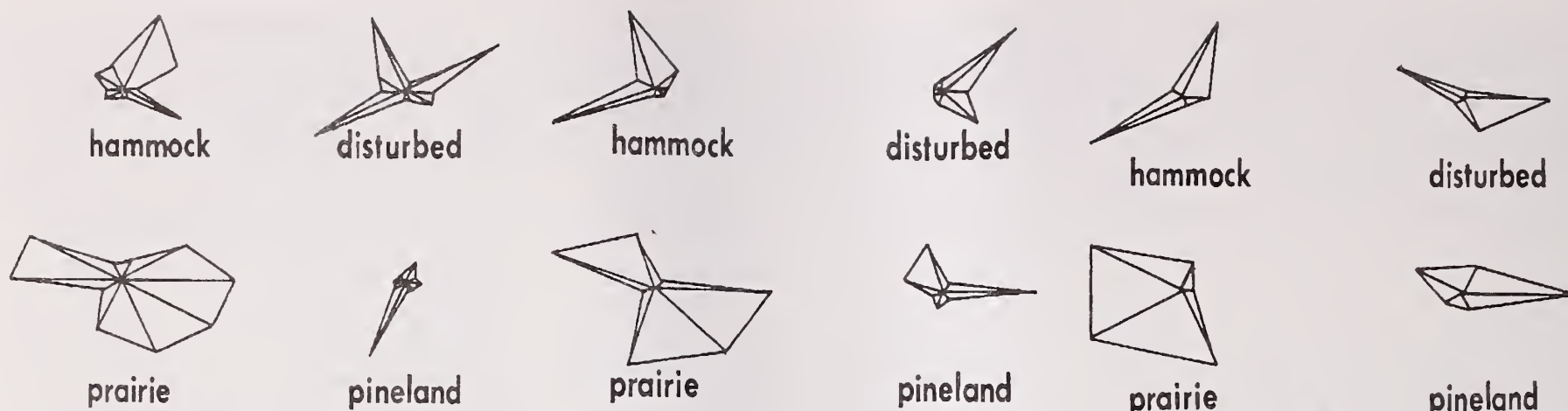


Figure 7.—Star plot diagrams of anuran data from table 3, comparing the frequencies of trapping (anurans per 1000 array days) of the species in the four habitat types. Genus and species names abbreviated on key at bottom of figure correspond to acronyms given in table 3.

Figure 8.—Star plot diagrams of lizard and turtle data from table 3, comparing frequencies of trapping (lizards or turtles per 1000 array days) in the four habitat types. Genus and species names abbreviated on key at bottom of figure correspond to acronyms given in table 3.

Figure 9.—Star plot diagrams of snake data from table 3, comparing frequencies of trapping (snakes per 1000 array days) in the four habitat types. Genus and species names abbreviated on key at bottom of figure correspond to acronyms given in table 3.

Pineland. *Sistrurus miliarius* was well represented in all habitats, but is least common in Hammocks. *Thamnophis sirtalis* was most abundant in Prairie, while *T. sauritus* was most common in Prairie and Hammocks. *Diadophis punctatus* is the snake species most difficult to keep in traps (because of their small size they could more readily escape) but current data indicate that they are most common in the leaf litter environment of Hammocks (fig. 9).

The most similar habitats with regard to trap data were Prairie and Pineland, the least similar were Pineland and Hammock (table 5). Table 5 includes the only data from the arrays and therefore some species are excluded from the similarity index (because the index used, Morisita's index (Horn 1966; Brower and Zar 1984) requires data on both the number of species and the number of individuals per species in the estimation of degree of similarity).

Discussion

Species List

Duellman and Schwartz (1958) gave a complete list of the localities from which they examined specimens but, unfortunately this list does not serve as an effective species list for this study. Since the intention of their study was a survey of all of southern Florida, they did not collect as exten-

sively in one area as we have been able to. Nevertheless, the descriptions of habitat preferences they gave make it clear that a few more species might be found in the Long Pine Key region if I continue the study. There are some noticeable absences from their list for the Long Pine Key and Paradise Key areas however: *Storeria dekayi* and *Diadophis punctatus*. It is possible that these species were merely overlooked in their surveys

Table 5.—Measures of similarity among arrays grouped by vegetation type based on data from table 3 (1984-1986, above). Numbers above the diagonal are the numbers of species shared between habitats; numbers along the diagonal, boldfaced, are numbers of species occurring in each habitat. Numbers below the diagonal, underlined, are Morisita's indices.

	Prairie	Pine	Hammocks	Disturbed
Prairie	30	21	20	17
Pine	<u>.736</u>	22	19	16
Hammocks	<u>.608</u>	<u>.308</u>	24	17
Disturbed	<u>.314</u>	<u>.253</u>	<u>.589</u>	21

and it is extremely unlikely that these species were not present in the local area thirty years ago (Duellman and Schwartz, personal communications).

Salamanders were the taxon most poorly represented in LPK, only four of the state's 24 salamanders were found in southern Florida (table 1), and only three of these were found in LPK. The reason for the low count is obviously the low elevation and poor soil development of the region.

The majority of Florida's salamanders are members of the family Plethodontidae, and this family is primarily distributed in the Appalachian mountains and foothills of the eastern U.S. Many species are stream dwellers, others are forest litter inhabitants that require a moist thick leaf litter and soil development. The mole salamanders, family Ambystomatidae, also require soils for burrowing. Moreover, salamander larvae are frequently absent from aquatic settings in which fish are common.

One notable exception is the newts (family Salamandridae), but even the one member of this family from the region, *Notophthalmus viridescens*, is rare. The only successful salamanders in the region are fully aquatic, neotenic, eel-like animals: *Amphiuma means*, *Siren lacertina* and *Pseudobranchius striatus*. Their cryptic life styles and easy access to the underground aquifer through the porous limestone bedrock may be important reasons for their success.

The number of anuran, lizard and turtle species are all rather low in southern Florida (tables 1 and 2). Several species of lizards extend southward past the mainland into the Florida Keys, but appear to have completely by-passed the western extension of the Miami Rock Ridge (in particular LPK) e.g. *Eumeces egregius* and *Cnemidophorus sexlineatus*. Two species are endemic to the sandhills and scrub habitats of Florida (*Sceloporous woodi* and *Neoseps reynoldsi*) and their absence in the area is again probably due to the lack

of suitable soils and substrates. The reason for the absence of the other two species of *Ophisaurus* (*O. attenuatus* and *O. ventralis*) listed by Duellman and Schwartz (1958) is not clear, although they did note that *Ophisaurus compressus* was the "most abundant" of the three species in southern Florida.

The only notable introduced lizard was *Anolis sagrei*. This species is so common in southern Florida now that it is no surprise that large populations are found in some parts of the current study area (Wilson and Porras 1983). In LPK it was generally limited to areas where there was a greater rate of contact with visitors, and in Disturbed settings. In remote Hammocks anoles were rarely observed, but Palma Vista I and Royal Palm Hammocks (both sites that are popular with visitors and adjoin roads) *Anolis sagrei* is extremely common, as well as throughout the hole-in-the-donut. At the current time the park appears to have a limited "load" of exotic lizards. *Hemidactylus garnoti* was observed at the parking lot at Pahayokee visitors site, and there are occasional reports of this species and of *Anolis equestris* in the LPK campground area and the "Pine Island" residential area for park staff.

Of the few specimens of *Gopherus polyphemus* seen during the study, the only one from the study area was crossing the road into the hole-in-the-donut (several others were seen in the Pine Island residential area and one shell was near a pond, but no one is certain of the source of these animals, and some visitors have been known to release gopher tortoises near the entrance to the park). Whether the sighting within the study area (the turtle was measured, and marked) is indicative of a small population or is a captive released by a visitor is not at all clear.

The presence of a population of gopher tortoises on Cape Sable (Kushlan and Mazzotti 1985) does not help in explaining the single

specimen, and Duellman and Schwartz (1958) list only one specimen for Dade County. Duellman and Schwartz (1958:260) described *Sternotherus odoratus* as "the least abundant of the three southern Florida kinosternids," and I have found it in the Shark River Slough region but not LPK. *Kinosternon subrubrum* is described by Duellman and Schwartz (1958:265) as avoiding "the main part of the Everglades, an area where *K. bauri* reaches its greatest abundance. When the above three rare species are noted the turtle list for Long Pine Key is typical of the southern Florida region.

Some of the species listed by Duellman and Schwartz were not common in the southern everglades, but were found in other areas of southern Florida. There were no species of anurans that I expected to find and did not. The burrowing nature of *Scaphiopus holbrooki* probably prevents it from being common in LPK, and it was never seen or heard during this study.

The crocodilian fauna of LPK is composed of only one species, the American alligator (although there have been rare occurrences of the American crocodile, *Crocodylus acutus*, in the freshwater reaches of the Taylor Slough drainage in the vicinity of the study area, W.B. Robertson, Jr. pers. comm). The alligator is found in almost every place in the everglades where there is water. We commonly found evidence of alligators in the seasonally flooded Prairie (alligator trails) and in the willow heads and Hammocks ("gator holes," a few nests seen, juvenile and adult alligators observed). The LPK region is certainly peripheral to the main distribution of the species in the park.

The snake fauna is clearly the best represented fauna in LPK. Of the 26 species listed for southern Florida, 21 were collected during the study. Of the five not found during this study only one was expected, *Seminatrix pygaea*, and the technique for trap-

ping this species described by Lorraine (1985) will be tried in the study area in the future. *Heterodon platyrhinos* was described by Duellman and Schwartz (1958) as not being abundant in southern Florida, and there is only one report of it from the LPK area (Roger L. Hammer pers. comm.).

Masticophis flagellum is still reported from the pineland remnants of southwest Dade County. Duellman and Schwartz (1958) had no records of this species from the park, but since then there has been one record from the park.

Pituophis melanoleucus was represented in the work of Duellman and Schwartz by a single specimen from Miami, and a single specimen of this species was collected in 1984 in North Miami Beach. The snake was probably a captive pet released in the area, since its feces contained white mouse remains (Robert J. Nodell, pers. comm.). *Tantilla oolitica* (*T. coronata wagneri* of Duellman and Schwartz) has never been recorded from the park, and its range is limited to isolated Atlantic Coastal Ridge remnants on the eastern coast and the Florida Keys (Wilson and Porras 1983).

Habitat Use and Preferences

Within the LPK region, Prairie habitat has the most diverse and abundant herpetofauna. The Prairie is a broad transition zone or ecotone between the longer hydroperiod Slough habitat and the drier Uplands, and they are seasonally inhabited by most species from those two habitats as well as a semi-aquatic fauna of their own.

Duellman and Schwartz (1958:206-213) characterized the habitats of southern Florida, as they pertain to Long Pine Key, as: Xeric (including the rocky Pineland of Long Pine Key), Mesic (including the tropical hardwood Hammocks of Long Pine Key), and Alternohygic (including

Prairie), and their characterization for each species is given in table 2.

All of the 18 species that Duellman and Schwartz (1958:211) characterized as generalists i.e. "common to all three" (i.e. Prairie, Pineland, and Hammock) were found in Long Pine Key. Seventeen of the 21 species (81%) they characterized as inhabitants of the Prairie (or Alternohygic habitat) were found in the study area.

Only 9 of the 22 species (40%) that Duellman and Schwartz (1958:210) characterized as Xeric or Pineland species are found in the region. Four of these 9 species were actually more common in Hammocks (*Eleutherodactylus planirostris*, *Sphaerodactylus notatus*, *Anolis sagrei*, and *Micrurus fulvius*), one (*Scincella laterale*) was common in Prairie, three were rare (*Gopherus polyphemus*, *Lampropeltis triangulum*, and *Cemophora coccinea*) and only one (*Crotalus adamanteus*) was actually most common in Pineland (see table 2).

Using the species associations of Duellman and Schwartz (1958), of the 51 species from Long Pine Key, 35% (18) are generalists, 33% (17) are Prairie species, 18% (9) are Pineland or Xeric in habitat association, 6% (3, *Limnaoedus ocularis*, *Pseudacris nigrita* and *Ophisaurus compressus*) are common to Prairie and Pineland, 6% (3, *Alligator mississippiensis*, *Trionyx ferox* and *Deirochelys reticularia*) are primarily Slough or Hygic (Duellman and Schwartz 1958:212), and 2% (1, *Osteopilus septentrionalis*) from Edificarian-Ruderal and Hammock (Mesic) habitats.

The limit to the preservation of overall diversity of the Long Pine Key region is the extent of rocky Pineland habitat, because it is the major habitat type of the area with the smallest percentage (40%) of its herpetofauna (as defined by Duellman and Schwartz 1958) represented. It is important to note that the common use of interdigitating finger glades, i.e. the local Prairie, and Hammocks by some of the Pineland species

makes it clear that overall diversity depends upon continued management to preserve the current patchiness of the area.

Sixty two percent of the species trapped in the Disturbed habitat are characterized as generalists by Duellman and Schwartz (1958), 14% are from Pineland and Prairie, 14% are from Pineland and 10% are from Prairie.

While the vast majority of amphibians and reptiles were either trapped and, or seen in the Disturbed habitat, a few were rarely or never seen in the Disturbed habitat: *Limnaoedus ocularis*, *Pseudacris nigrita*, *Scincella laterale* and *Sphaerodactylus notatus*. In contrast to these native species, which were not common to the Disturbed habitat, the two exotic species, *Osteopilus septentrionalis* and *Anolis sagrei* were most common there.

Species composition of the Disturbed habitat primarily depends on the historical topography of the area. The vast majority of species there are generalists, but the area is large enough that local variations in hydroperiod attract a number of species more commonly associated with drier or wetter conditions and future analyses of this very complex area will involve a more specific separation of habitat types within the area. Clearly, most of the species of amphibians and reptiles are responding to basic microhabitat requirements that have little to do with the actual species composition of the vegetation (Campbell and Christman 1982a:170-171).

Abundance

It is impossible to accurately compare the trapping results of this study to other studies. The methods, objectives and local circumstances of each study vary widely. Perhaps most confounding is the variability in the number of months per year during which species are active, and this

makes comparisons based on animals per check day difficult. There are also differences in types of arrays used, the purposes of the trapping effort, substrate characteristics and ability to use pit traps, all of which preclude valid comparisons.

Campbell and Christman (1982b) summarized their results from northern Florida, in which they operated 30 arrays for 7432 array-days. They collected 1644 animals of 43 species from 11 habitats for an average of 0.22 animals per array-day. In LPK, 13 arrays operated a total of 9792 array-days and collected 1709 animals of 37 species in 4 habitats for an average of 0.18 animals per array day, a similar catch rate per array day.

Campbell and Christman (1982b) used both funnel traps and pit traps, and they estimated that only 36% of their collection came from funnel traps. They also state that 69% of the animals trapped were *Eleutherodactylus planirostris*, and that 90% of their trappings were of *E. planirostris* and *Gastrophryne carolinensis*. Both of these species were readily trapped in their pit traps. If their pit trap excluded, and look at the percent from funnel traps, there was a much trap yield.

There are so many differences in the two studies that the only conclusion to be drawn is that the results compare favorably with that the LPK region has a moderate diversity and comparable abundance of animals, based upon similar trapping effort.

Comparisons to other studies are even more difficult, since studies in more temperate climates are done only during the warmer months of the year. For example, Clawson and Baskett (1982), in Missouri, used 13 arrays a total of 3159 array days in the spring, summer, and fall, and captured 2545 animals, for an average of 0.81 animals per array day. This much higher figure may well be representative of the greater concentration of both animals and resources typically found in more temperate climates.

Species Diversity

Species richness for southern Florida was described by Duellman and Schwartz (1958:205) as "depauperate" and "impoverished." They state that "an impoverished herpetofauna is what might be expected at the end of a long peninsula, through the length of which certain habitats and their inhabitants disappear."

The difficulty in evaluating this statement arises from the fact that there is much more involved in the biogeography of the peninsula of Florida than a simple "peninsula effect" due to reduced area and distance from centers of distribution (Robertson and Kushlan 1984). There is also the recent geological origin of the land area, the poor development of soils in the area during the time since emergence, the lack of variation in relief of the area (Olmsted and Loope 1984), and the severe human disturbance. All of these factors need to be considered in evaluating the possible reasons for an "impoverished" fauna. Finally there is the issue of deciding whether the fauna deserves the label of "impoverished" in the first place.

A reduced species list does not by itself determine whether the biomass of the existing species is high or low, e.g. while the species list for fresh water fish is considered low for the area (Loftus and Kushlan 1987) they are the principal food of an enormous biomass of wading birds. Robertson and Kushlan (1984:234) have addressed this point: "...the nearly unique ability of the South Florida ecosystem to support such large numbers of 14 species of superficially similar secondary and tertiary consumers on a resource base that is reduced in species diversity by biogeographic factors is generally unappreciated." and the nesting efforts (1972 or 1974 numbers) of the White Ibis and Wood Storks alone are estimated to have required "in excess of 3 billion kilocalories or approximately 2500 metric tons of food..."

As the impact of the remaining 12 species of wading birds is not known and the secondary productivity of South Florida habitats has not yet been studied, the meaning of this energy requirement to the total system is undeterminable."

During this study we have collected data on 51 species of amphibians and reptiles (table 2). This is not a low figure for an area the size of LPK (8000 ha).

Vogt and Hine (1982) list 34 species of amphibians and reptiles from their study area in southern Wisconsin. Clawson and Baskett (1982) list 35 species from their Missouri study area. Clarke (1958) lists 39 species from Osage County, Kansas. In trapping studies in the Florida sandhills of Tampa, Mushinsky (1985) lists 27 species. Campbell and Christman (1982b) list 60 species from their extensive study in northern Florida, and this number comes from a variety of sampling techniques in, at least, 11 different habitat types.

Gibbons and Harrison (1981) list 68 species from coastal mainland South Carolina and Gibbons and Patterson (1978) list 94 species from the Savannah River Plant in South Carolina. Myers and Rand (1969) list 100 species for Barro Colorado Island, Panama. Crump (1971) lists 116 species for the Belem area of Brazil.

From the temperate to tropic latitudes there is an obvious increase in overall diversity, but the species richness for the LPK is not very low for its latitude. The presence of 51 species and the fact that many are abundant makes it clear that the application of terms such as impoverished or depauperate must be used in context. Rather than pondering the absence of some species (especially when for the group with the least representation in the area, the salamanders, it is quite clear why they are not common, see above) I find myself, like Robertson and Kushlan (1984, above), more impressed with the actual abundance of animal life in this unique area.

Conclusions

1. The species list for the LPK includes at least 51 species, 15 species of amphibians and 36 species of reptiles. The most poorly represented group is the salamanders, the best represented group is the snakes. The survey of current species composition is basically the same as reported 30 years ago for the area by Duellman and Schwartz (1958). The fact that there has been no reduction in species richness of the local area should be considered a major benefit of the preservation of the region inside the national park.
2. Amphibians and reptiles of LPK are primarily habitat generalists, usually being found in three of the four major habitat types in the area. The principal separation by habitat is related to the characteristics of the substrate, there being a subset of herptiles most commonly found in areas with greater soil development (Hammocks and the Disturbed areas) and another subset of herptiles that are more common in seasonally flooded Prairie. The most poorly represented group is that described as primarily from Xeric, Pineland habitat, and the absence of sandy soils in the rocky Pineland makes this the most fragile component of the Everglades herpetofauna. The findings of this study do not differ significantly from those of Duellman and Schwartz (1958) from thirty years ago. The results point out that there is a significant portion of the local herpetofauna that relies upon the preservation of large contiguous areas of native Pineland interspersed with Hammocks and seasonally flooded Prairie for its continued success.
3. Phenologies of amphibians and reptiles of the LPK can be described as modified temperate zone patterns. While the subtropical character of the southern coastal portion of peninsular Florida results in a year long growing season, with only occasional frosts, the seasonality of rainfall and the temperate zone origin of the herpetofauna results in a traditional spring emergence of the herptiles, tied to increasing day length, warmer temperatures and the onset of heavy rainfall.
4. Estimates of density and relative abundance remain difficult to give at the current time. Comparison of current trapping results with those of Campbell and Christman (1982a, 1982b) from 11 habitats in northern Florida indicate a similar level of abundance for the two areas, but differences in the actual species lists, habitat types and methodologies make such conclusions tenuous. Comparisons of the fauna of the area with those of a wide variety of other regions indicate that the herpetofauna of LPK, with the exception of the salamanders, has a moderate level of diversity.

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The Herpetofaunal Community of Temporary Ponds in North Florida Sandhills: Species Composition, Temporal Use, and Management Implications¹

C. Kenneth Dodd, Jr.² and Bert G. Charest³

The sandhills and xeric live oak herpetofauna of Florida is diverse and contains a number of endemic species. Whereas the terrestrial herpetofauna has been described for a few sandhills communities (Campbell and Christman 1982, Mushinsky 1985), there have been no long-term studies of the ecology of species using temporary ponds. For breeding amphibians, sandhills temporary ponds are often the only sources of water that are free of predatory fish and many larger predatory insects, and such ponds may be extremely important for amphibian reproductive success (Macan 1966, Sexton and Phillips 1986, Semlitsch 1987, Moler and Franz 1988). At the same time, the ephemeral nature of these breeding sites makes reproductive success uncertain and thus provides an opposing selective pressure for their use (Semlitsch 1987).

Since January 1985, we have been conducting studies on the herpetofaunal community at a temporary pond in a north-central Florida longleaf pine-turkey oak ("high pine")

sandhills. Little is known of the composition of such Florida herpetofaunal communities, although Moler and Franz (1988) reported 16 anuran species breeding in various types of wetlands surrounded by sandhills on the 3750 ha Katharine Ordway Preserve-Swisher Memorial Sanctuary in Putnam County. Nothing is known about movement patterns and activity cycles of the herpetofauna, or about the numbers of individuals breeding at such ponds and the numbers of offspring produced.

The purposes of our study are to gain insight into the structure of the herpetofaunal community using a temporary pond in a sandhills ecosystem, to assess variation in species composition and temporal use of the pond, and to gather basic biological information on the species that comprise the community. This paper presents findings based on two years of fieldwork of a projected five year study.

Methods

Breezeway Pond, a 0.16 ha isolated temporary pond in a shallow 1.3 ha basin on the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County, Florida, was encircled with a 230 m drift fence (mean height = 36 cm above the substrate) following the general procedure of Gibbons and Semlitsch (1982), reviewed by Jones (1986a).

Abstract.—Amphibians and reptiles use an isolated temporary wetland in a north Florida sandhills throughout the year despite variation in environmental conditions. Species composition and number of individuals varies seasonally and annually. Temporal variation in habitat use must be considered in managing small wetlands and assessing their importance to the herpetofaunal community.

Buckets were spaced at 10 m intervals and paired on opposite sides of the fence, making 23 stations of two buckets each. Sloping covers were put over the buckets and wet sponges were placed in them to minimize exposure to direct rays of the sun and desiccation, respectively. As a result, mortality among captured animals was < 1.0% and was caused primarily by invertebrate predation (spiders, ants, centipedes, and beetles).

Breezeway Pond is located at an ecotone. To the immediate south and west, the predominant habitat is "high pine" sandhills dominated by longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) and wiregrass (*Aristida stricta*). A xeric hammock dominated by sand live oak (*Q. geminata*) and laurel oak (*Q. laurifolia*) faces the north, while a small "Panicum meadow" dominated by maidencane (*Panicum hemitomom*), lies to the east. The distance from the drift fence to the nearest forested plant association is no more than about 50 m in any direction.

Buckets were checked 5 days per week in the morning (beginning 0700-0900 h depending on season) from January 16 through April 12, 1985, and from October 1, 1985, until September 30, 1987. For purposes of discussion and analysis, a year refers to a 12-month period from October through the following September (e.g. 1986 = October 1985 through September 1986) because reproduc-

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tion and metamorphosis generally cease in early autumn while winter breeding has yet to commence.

All reptiles and amphibians were measured in the field (snout-vent length, carapace and plastron length [for turtles], tail length [for snakes and glass lizards]), weighed and marked for future identification using a year code (e.g., 0022 identifies animals marked in 1986) or an individual identification number (all turtles, snakes, gopher frogs [*Rana areolata*], red-tailed skinks [*Eumeces egregius*], and ground skinks [*Scincella lateralis*]). Very small animals, mostly juvenile frogs and lizards, were not marked because of their extremely small toes.

Notes were recorded on tail regeneration and damage, breeding and hatchling coloration, and reproductive status. All animals, except lizards, were released on the opposite side of the fence from site of capture; lizards were released on the same side as captured. Weather conditions, rainfall, pond water level, and maximum and minimum air and water temperatures were recorded. These data are similar to those recorded in other long-term studies employing drift fences to study amphibian communities (Gibbons and Bennett 1974, Gibbons and Semlitsch 1982) and are vital to the inventory and management of ecological communities and individual species (Jones 1986b).

In this paper we concentrate our analyses on the two most commonly captured amphibians, the striped newt (*Notophthalmus perstriatus*), a species listed as of special concern in Florida (Christman and Means 1978), and the eastern narrow-mouthed toad (*Gastrophryne carolinensis*), a common Florida frog (Carr 1940).

We also divided the year into bi-weekly sampling periods and plotted the cumulative number of species captured versus sampling period. The three years were plotted separately. Data from October 1985 through September 1987 were treated

two ways: (1) as if sampling began in October, and (2) as if sampling began in April. This provided a between year comparison of how effective sampling for species numbers would be if sampling began in the autumn as opposed to the spring.

Statistical Analysis

Variation in the overall biweekly capture of amphibians and reptiles between 1986 and 1987 was compared using a Chi-square contingency table. The Spearman Rank Correlation Matrix then was used to compare bucket capture frequency between first capture and recaptured individuals, in both 1986 and 1987, of *G. carolinensis* and *N. perstriatus*. Since there were no significant differences, captures and recaptures were combined in subsequent analyses.

We tested for within-year variation in capture frequency inside and outside the fence using a one sample Chi-square goodness of-fit-test. The Spearman Rank Correlation Matrix was again used to make the following comparisons: (1) a within year comparison of animals captured inside the fence with those captured outside the fence for both 1986 and 1987 [both species], (2) a comparison of juvenile with adult *G. carolinensis* in 1986, (3) a comparison of juvenile *G. carolinensis* inside and outside the fence, and (4) a between year comparison of animals captured per bucket inside or outside the fence [both species].

To determine if *N. perstriatus* and *G. carolinensis* preferentially oriented to or from one of the three habitat types surrounding the pond, data were collapsed and analyzed using a Kruskal-Wallis 1-way ANOVA. Buckets 1-3 and 21-23 faced a xeric hammock, 4-6 faced a small open field, and 7-20 faced sandhills, thus producing the three habitat categories.

Statistical analyses were carried out using the SAS program for

microcomputers (SAS Institute Inc. 1985) or program ABSTAT version 4.09 (Anderson-Bell 1984). For all analyses, $P < 0.05$ was considered indicative of statistical significance.

Results

Environmental Conditions

Severe cold weather and a prolonged drought characterized the sampling period from January through April 1985. In Gainesville, 33 km west of Breezeway Pond, low temperatures reached -12 C and rainfall was 152.4 mm below normal for the three month period. Breezeway Pond was dry throughout this period. Summer rains filled the pond in mid-July, and water remained until December 16; maximum pond depth was 60 cm but declined steadily after September. Free water was present from January 10-February 3 and from March 14 to April 22, 1986. The pond remained dry throughout the summer of 1986 despite summer thunderstorms and did not refill until February 24, 1987. From then until June 20 (115 days), up to 60 cm of water filled the pond. On June 20, the pond dried and remained dry through September 30.

Species Composition

Thirty-nine species (7161 individual captures) used the pond or its periphery at some point during the 27 months that the traps were monitored (table 1). The amphibians captured most often were the winter/spring breeding striped newt, *Notophthalmus perstriatus*, and the spring/summer breeding eastern narrow-mouthed toad, *Gastrophryne carolinensis*. Only one other salamander was collected at Breezeway Pond, the dwarf salamander, *Eurycea quadridigitata*. Fourteen species of frogs visited the pond, and six were present at virtually any time of the year: *Acris gryllus*, *Bufo quercicus*, *B. ter-*

restris, *G. carolinensis*, *Limnaeodius ocularis*, and *Scaphiopus holbrooki*. Adult *Hyla femoralis* and juvenile *Rana*

catesbeiana were caught mainly in the summer. Adult *R. areolata* were caught in the early spring as they

moved toward breeding ponds, and juvenile *R. areolata* and *R. sphenoccephala* were caught in late summer and early autumn presumably as they emigrated to terrestrial habitats.

The most commonly captured reptiles were the lizards *Scincella lateralis*, *Cnemidophorus sexlineatus* and *Eumeces egregius*, and the snake *Seminatrix pygaea* (table 1). Recent hatchlings accounted for all individuals of the lizards *Ophisaurus ventralis* and most *S. lateralis*, as well as the snakes *Coluber constrictor*, *Nerodia fasciata* and *Thamnophis sirtalis*, and the turtles *Pseudemys floridana* and *Kinosternon subrubrum*. The only snake caught in substantial numbers was the swamp snake, *S. pygaea*, especially as they left the pond during the 1985 drought.

Table 1.—Species and numbers of individual amphibians and reptiles captured (first number) and recaptured (second number) at Breezeway Pond, January 1985 through September 1987. * = very small individuals not marked.

Species	1985 (January- April)	1985-1986 (October- September)	1986-1987 (October- September)	Total
Salamanders				
* <i>Eurycea quadridigitata</i>	5/0	10/0	8/0	23/0
<i>Notophthalmus perstriatus</i>	29/5	558/309	744/226	1331/540
Frogs				
* <i>Acris gryllus</i>	5/0	74/5	64/1	143/6
<i>Bufo quercicus</i>	1/0	111/31	96/50	208/81
<i>Bufo terrestris</i>	6/2	65/46	109/109	180/157
<i>Eleutherodactylus planirostris</i>	0/0	0/0	2/0	2/0
* <i>Gastrophryne carolinensis</i>	2/0	1500/226	379/274	1881/500
<i>Hyla chrysoscelis</i>	0/0	1/0	0/0	1/0
<i>Hyla femoralis</i>	0/0	4/0	39/2	43/2
<i>Hyla squirella</i>	0/0	3/0	0/0	3/0
* <i>Limnaeodius ocularis</i>	14/0	20/0	49/0	83/0
<i>Rana areolata</i>	2/1	9/5	46/23	57/29
<i>Rana catesbeiana</i>	2/4	9/4	0/0	11/8
<i>Rana grylio</i>	1/0	0/0	5/0	6/0
<i>Rana sphenoccephala</i>	0/0	5/0	15/2	20/2
<i>Scaphiopus holbrooki</i>	1/1	66/19	165/92	232/112
Turtles				
<i>Apalone ferox</i>	0/0	6/4	0/0	6/4
<i>Deirochelys reticularia</i>	0/0	2/0	0/0	2/0
<i>Kinosternon subrubrum</i>	9/0	7/0	11/4	27/4
<i>Pseudemys floridana</i>	0/0	17/14	2/2	19/16
Lizards				
<i>Cnemidophorus sexlineatus</i>	18/7	140/135	122/115	280/257
* <i>Eumeces egregius</i>	14/2	54/8	30/4	98/14
<i>Eumeces inexpectatus</i>	0/0	0/0	1/0	1/0
* <i>Ophisaurus ventralis</i>	0/0	14/2	15/0	29/2
<i>Sceloporus undulatus</i>	4/0	7/2	2/0	13/2
* <i>Scincella lateralis</i>	23/0	217/2	207/2	447/4
Snakes				
<i>Cemophora coccinea</i>	1/1	2/0	2/0	5/1
<i>Coluber constrictor</i>	2/0	7/0	8/8	17/8
<i>Diadophis punctatus</i>	0/0	2/0	2/2	4/2
<i>Micrurus fulvius</i>	0/0	6/0	8/0	14/0
<i>Nerodia fasciata</i>	3/0	4/1	13/1	20/2
<i>Nerodia floridana</i>	1/0	6/1	4/0	11/1
<i>Regina alleni</i>	2/1	1/0	2/0	5/1
<i>Seminatrix pygaea</i>	59/14	18/10	13/11	90/35
<i>Sistrurus miliarius</i>	0/0	4/0	2/1	6/1

Cumulative Capture Rates

The rate at which species were captured varied between 1986 and 1987 (fig. 1). More species were captured at a faster rate in 1986 than in 1987 for sampling begun in October. However, the reverse was true for sampling begun in April. In autumn, the number of new species reached an asymptote after about six weeks of sampling in both years but at different levels (25 in 1986, 23 in 1987). In spring, the capture of new species rose steadily both years; in 1986 it never leveled off whereas in 1987 it leveled off (at 31) only after four months of sampling. In 1985, the rate at which new species were observed rose rapidly throughout the period and was beginning to level off only when the observations were terminated.

In 1985, three months of sampling produced 25 of the 39 (64%) species now known to be present at Breezeway Pond. Corresponding percentages for other years and durations of sampling are as follows: 1986 - 6 months begun in October = 74%, 6 months begun in April = 77%, 12 months = 85%; 1987 - 6 months be-

gun in October = 59%, 6 months begun in April = 82%, 12 months = 87%.

Variation in Biweekly Capture

The numbers of amphibians and reptiles captured biweekly varied and was significantly different between 1986 and 1987 for both amphibians ($X^2 = 1366.46$, 1 df, $P < 0.001$) and reptiles ($X^2 = 128.08$, 1 df, $P < 0.001$). For amphibians, very few were caught from October 1986 through January 1987 compared with the same period in 1985-1986. There also were many fewer individuals caught during the summer of 1987 compared with 1986. This was due to a late summer drought which resulted in the complete drying of the pond with subsequent reproductive failure of *G. carolinensis*. Successful reproduction by this species in the summer of 1985 accounted for the large numbers of amphibians captured in 1986 (fig. 2). Even if juvenile narrow-mouthed toads are excluded ($N = 690$), there were still nearly 1000 more amphibians recorded in 1986 compared with 1987 (3425 in 1986, 2475 in 1987).

The numbers of reptiles recorded in and around Breezeway Pond were very similar between years, although there was enough variation to make the patterns significantly different. As might be expected, reptile activity decreased during the winter from late October through mid-March although some individuals were active year round (fig. 3). The peak in numbers in mid-July 1986 represents both a large number of species captured as well as an influx of hatchling *S. lateralis*.

Temporal Capture Variation: *Notophthalmus perstriatus* and *Seminatrix pygaea*

An example of annual variation in numbers of individuals and dates of

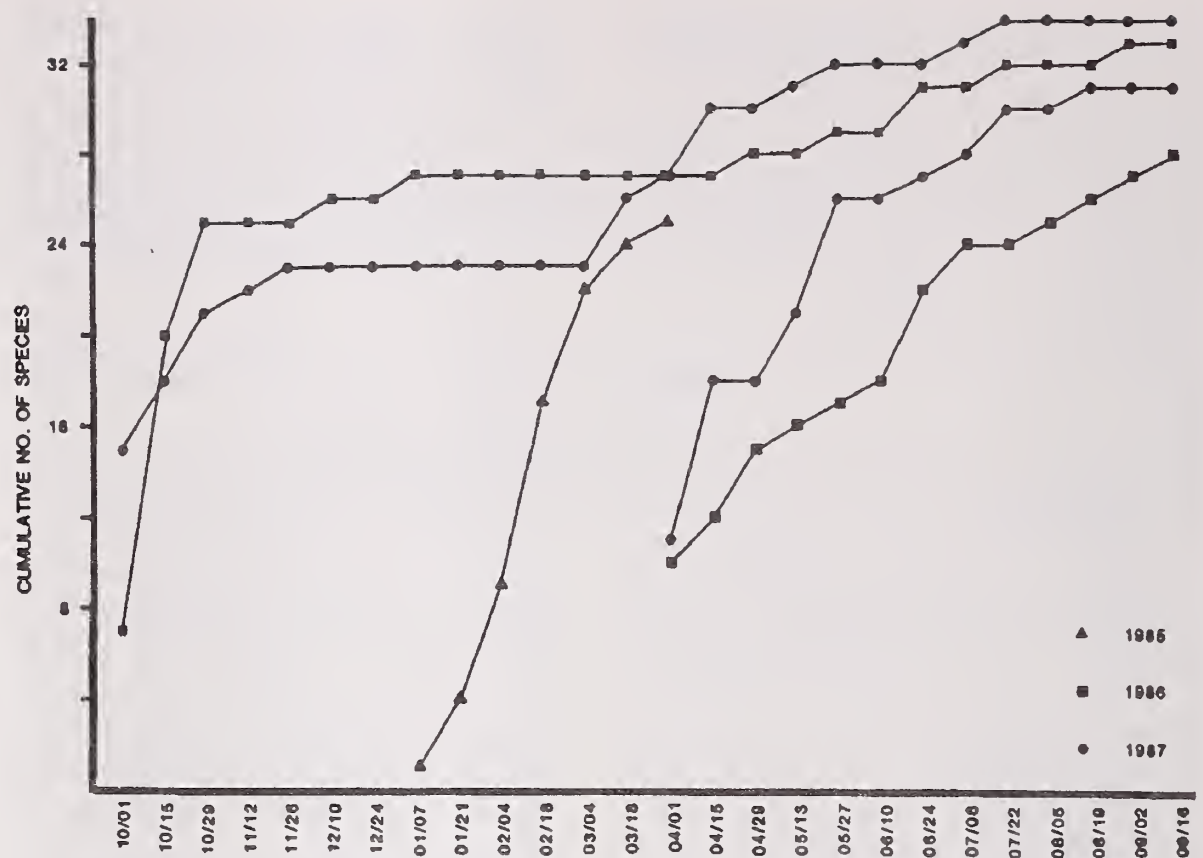


Figure 1.—A comparison of the rate at which species were recorded for sampling from January-April 1985 (1985), October 1985-September 1986 (1986), and October 1986 through September 1987 (1987). For 1986 and 1987, the data were treated as if sampling began either in October or April.

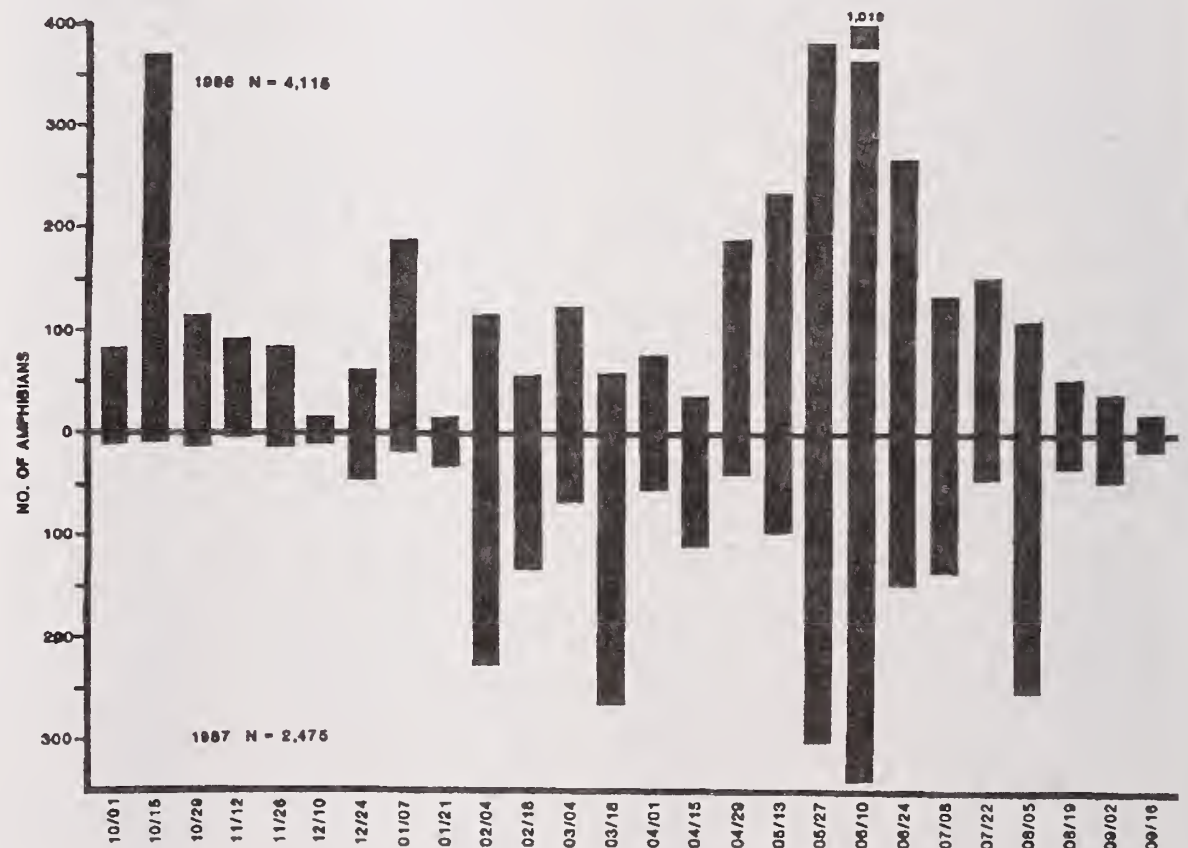


Figure 2.—Number of amphibians captured at Breezeway Pond in 1986 and 1987 by 2-week intervals.

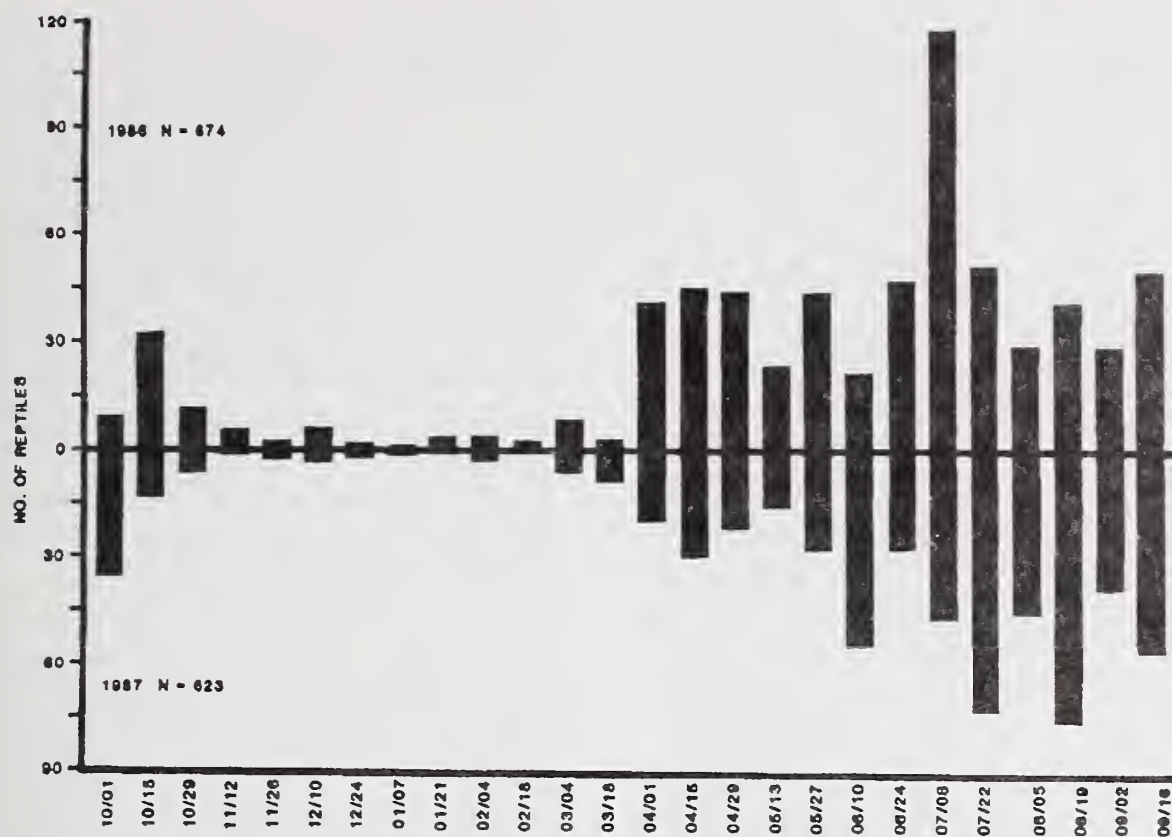


Figure 3.—Number of reptiles captured at Breezeway Pond in 1986 and 1987 by 2-week intervals.

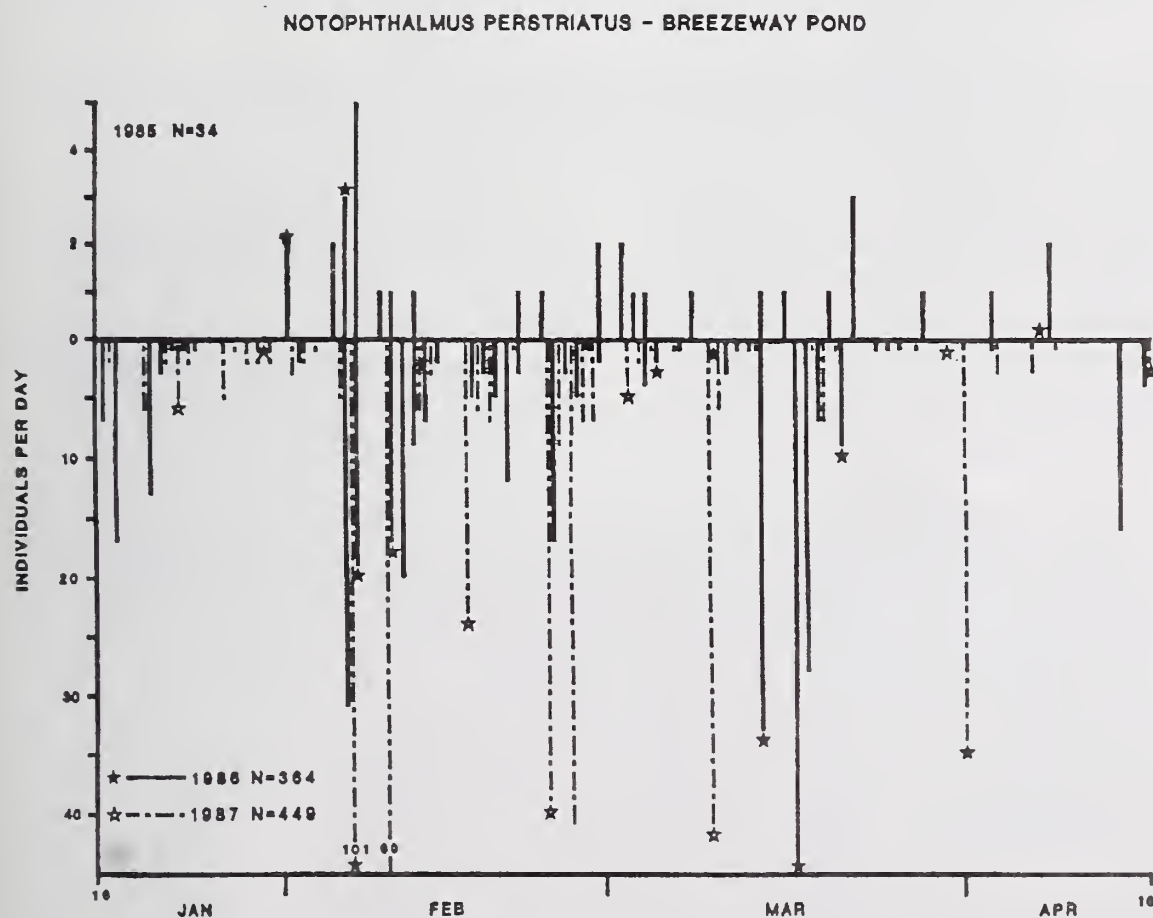


Figure 4.—Comparison of the numbers of striped newts (*Notophthalmus perstriatus*) captured from January 16 through April 16, 1985-1987. The stars indicate days of > 10 mm rainfall.

capture is illustrated by comparing collecting data from 1985 through 1987 for striped newts, *N. perstriatus* (fig. 4), and swamp snakes, *S. pygaea* (fig. 5). From mid-January through mid-April, the numbers of newts captured varied from 34 in 1985 to 364 in 1986 and 449 in 1987. Most captures occurred from the first week of February through the latter part of March, and were associated with rainfall > 10 mm. Movements in 1985 occurred despite bitter cold and prolonged drought.

In contrast, striped swamp snakes did not leave the pond during the cold weather of 1985, but waited until temperatures moderated in early March (fig. 5). Unlike newts, however, they did not return in appreciable numbers later in 1986 or 1987 despite favorable habitat and climatic conditions.

Orientation and Movement Patterns: *Gastrophryne carolinensis* and *Notophthalmus perstriatus*

The frequency of bucket capture, both inside and outside the drift fence, varied significantly for both adult *G. carolinensis* and *N. perstriatus* in 1986 and 1987 (table 2). These data indicate non-random movement into and out of the pond. There was no significant correlation between inside and outside bucket capture frequency for *G. carolinensis* in 1986 ($r_s = -0.20$, 22 df) or 1987 ($r_s = -0.25$, 22 df). There was significant correlation between inside bucket captures between 1986 and 1987 ($r_s = 0.35$, 22 df) but not between outside bucket captures between years ($r_s = 0.06$, 22 df). These results indicate that narrow-mouthed toads left the pond in similar directions but entered it from different directions.

Juvenile *G. carolinensis* entering and exiting Breezeway Pond showed distinct differences between capture frequency at different stations ($X^2 = 535.73$, df = 22, $P < 0.001$). However,

they showed no correlation with adult capture frequency per station ($r_s = 0.09$, 22 df). There also was no correlation in bucket capture frequencies for juveniles caught inside and outside the drift fence ($r_s = 0.26$, 22 df). These data apply only to 1986 because no juveniles were observed in 1987.

For *N. perstriatus*, there was likewise no significant correlation in inside versus outside bucket capture frequency in 1986 ($r_s = 0.23$, 22 df) or 1987 ($r_s = 0.03$, 22 df). Capture frequencies were compared outside the fence in 1986 versus 1987 ($r_s = 0.07$, 22 df, $P > 0.05$) and inside the fence in 1986 versus 1987 ($r_s = 0.55$, 22 df, $P < 0.01$). As with *Gastrophryne*, these results suggest that newts were leaving the pond in similar directions between years, but that they were entering it from different directions.

Habitat Relationships

Adult *Gastrophryne* did not move toward specific habitats in either 1986 ($X^2 = 2.62$, 2 df, $P = 0.27$) or 1987 ($X^2 = 0.32$, 2 df, $P = 0.85$). On the other hand, juvenile narrow-mouthed toads moved toward the sandhills at a higher frequency than would be expected if movements were random ($X^2 = 13.31$, 2 df, $P = 0.001$), but not toward the pond from any particular direction ($X^2 = 2.26$, 2 df, $P = 0.32$). Striped newts showed non-random movement in 1986 ($X^2 = 7.79$, 2 df, $P = 0.02$) toward the sandhills but in 1987 moved toward the *Panicum* meadow more often than would be expected by chance alone ($X^2 = 9.42$, 2 df, $P = 0.009$). Movement in relation to nearby habitat is illustrated in figure 6.

Discussion

Was Sampling Effective?

Although we caught 39 species in > 7000 captures, it is likely that more

SEMINATRIX PYGAEA - BREEZEWAY POND

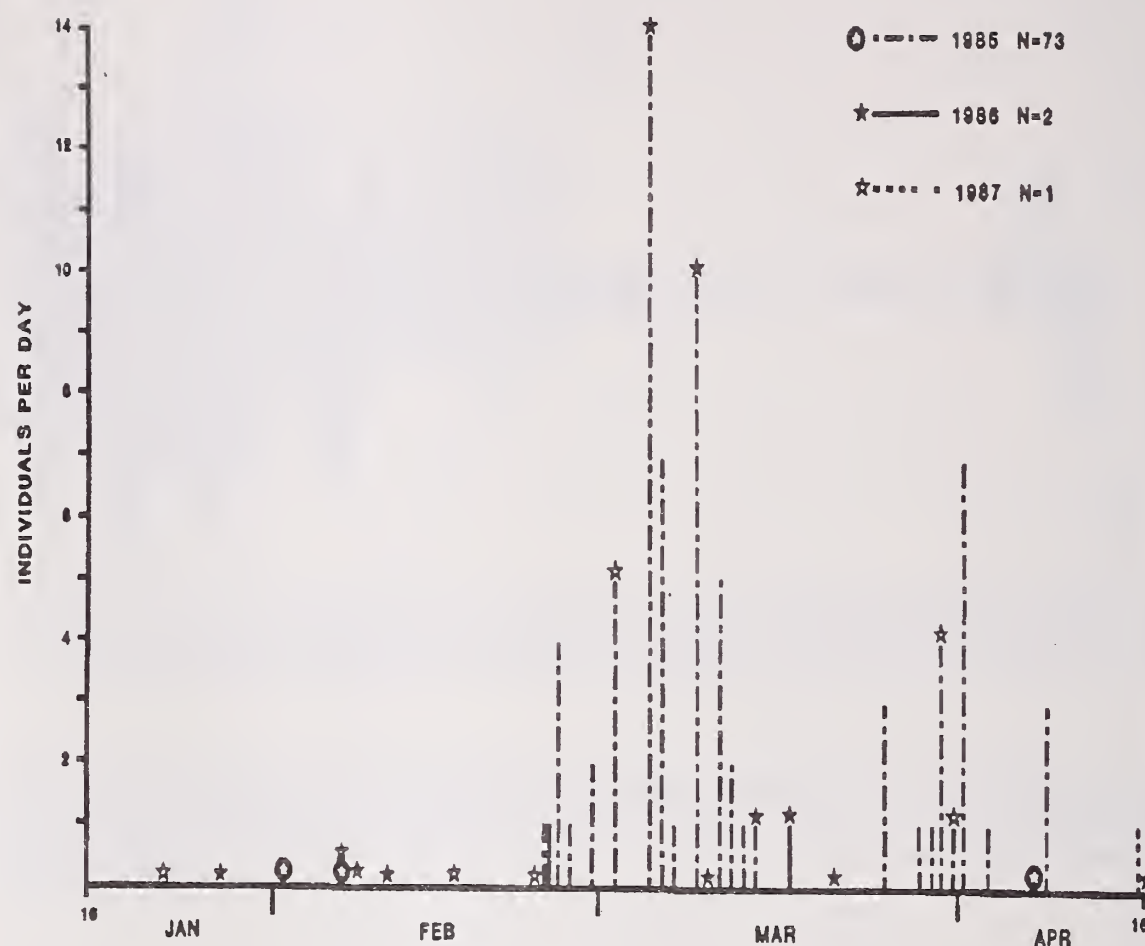


Figure 5—Comparison of the numbers of swamp snakes (*Seminatrix pygaea*) captured from January 16 through April 16, 1985-1987. The stars indicate days of > 10 mm rainfall.

species of amphibians and reptiles occasionally visit Breezeway Pond. Some species, such as the eastern coachwhip snake (*Masticophis flagellum*), Florida pine snake (*Pituophis melanoleucus*), and gopher tortoise (*Gopherus polyphemus*), are common

in adjacent sandhills but have not been observed in or near the pond. Large snakes (e.g., *Pituophis*, *Masticophis*) could easily go over the fence and thus avoid capture. The barking treefrog (*Hyla gratiosa*) bred in the pond before the initiation of our

Table 2.—Is the frequency of bucket capture random inside and outside the drift fence? For all analyses, there were 23 stations and 22 df. A significant value indicates non-random movement.

Species	Year	Orientation	X ²	P
<i>Gastrophryne carolinensis</i>	1986	Inside	55.68	< 0.001
	1986	Outside	81.25	< 0.001
	1987	Inside	84.00	< 0.001
	1987	Outside	100.69	< 0.001
<i>Notophthalmus perstriatus</i>	1986	Inside	243.56	< 0.001
	1986	Outside	93.44	< 0.001
	1987	Inside	88.45	< 0.001
	1987	Outside	145.48	< 0.001

study (R. Franz, pers. comm.), but we have never captured it or heard it calling from the pond.

Some species, particularly treefrogs such as *Hyla femoralis*, might be able to climb over the fence and thus go undetected (Gibbons and Semlitsch 1982). Newts (*N. viridescens*) are known to scale drift fences (Semplitsch and Pechmann 1985) although we have not observed *N. perstriatus* doing so. We have observed a substantial number of unmarked newts inside the drift fence even after two years of study, but we do not know if they were residents that were moving after remaining in the pond area for several years, or if they entered by crawling over or under the drift fence. Harris et al. (1988) noted that many adult *N. viridescens* burrowed into mud at the edge of North Carolina sandhills ponds as the ponds dried.

For these reasons, our data probably underrepresent both the number of species and individuals using the pond during the two years of observation. On the other hand, it is unlikely that some species (e.g., *Bufo*, *Scaphiopus*) are able to climb the fence. As such, capture results of these species may provide a reasonably accurate estimate of pond use.

Activity Patterns

It is difficult to interpret data on activity patterns of species with only two years of data because there are many variables that influence activity cycles and the timing of reproduction. These variables, such as rainfall amount and distribution, maximum and minimum temperatures, and hydroperiod (Wiest 1982, Semlitsch 1985, Pechmann et al. 1988), vary daily, seasonally and yearly, and may affect different species in different ways. The subtle interaction of these parameters probably accounts for the variation in activity patterns observed between years (Semplitsch 1985, Semlitsch and Pechmann 1985).

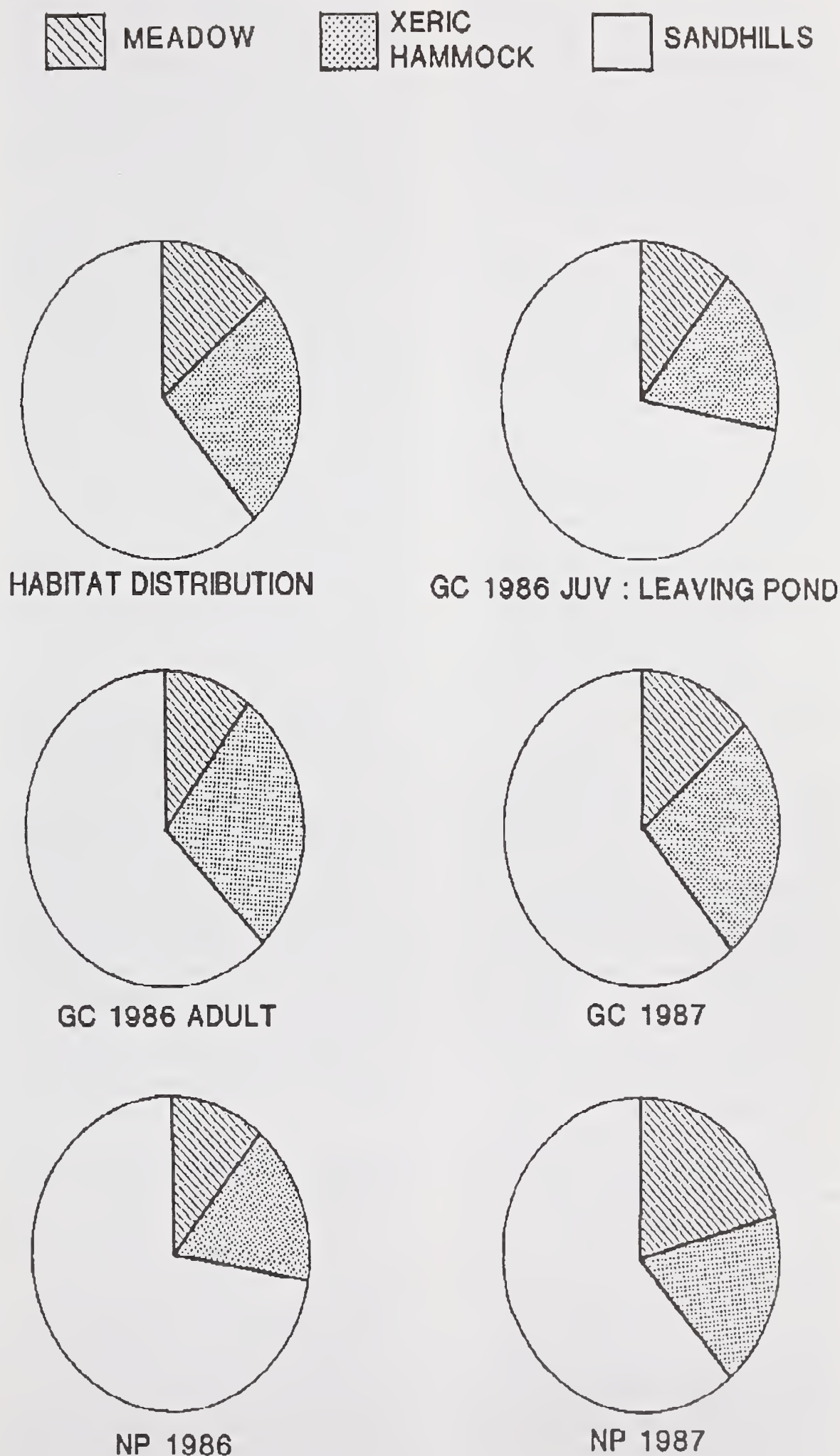


Figure 6.—Diagram illustrating the relationship between buckets, emigration from the pond, and nearby habitat for *Gastrophryne carolinensis* (GC) and *Notophthalmus perstriatus* (NP).

Amphibians breeding in sandhills ponds are faced with substantial uncertainty as to whether or not suitable conditions will prevail for reproduction. Breezeway Pond was chosen as the site for our study because it had consistently held water from the spring of 1983 through January 1985 (R. Franz, pers. comm.). Beginning in January, climatic conditions changed resulting in two years of drought with only sporadic free water. Temporary ponds may allow reproduction free of certain predators, but their use comes at the cost of reproductive uncertainty.

Amphibians are active during or immediately after periods of rainfall or high humidities. However, the interaction of moisture and temperature and how they affect condensation probably affects diel activity (Semlitsch and Pechmann 1985, Duellman and Trueb 1986, Pechmann and Semlitsch 1986) but also seasonal activity.

The extremely dry conditions at Breezeway Pond during the study makes it difficult to predict whether patterns observed in early 1985 and from late 1985 through late 1987 are "typical" for the amphibian community using the pond. Observations from other long-term studies of herpetofaunal communities suggest that there is wide variation in numbers of individuals at a site and in reproductive success from year to year (Gill 1978, Semlitsch 1983, 1985, 1987, Pechmann et al. 1988).

Because of their lack of dependence on standing water, temperature is probably more important than hydroperiod in governing reptile daily and seasonal activity, at least for species in direct spatial proximity to the pond. However, reptile predators that opportunistically visit temporary ponds, such as garter snakes (*Thamnophis* sp.), might increase the number of visits and duration of stay if a sufficiently long hydroperiod allows amphibian reproduction to take place. Our data are insufficient as yet to answer this question.

Some individuals are active even during unfavorable environmental conditions of drought and unseasonably cold temperatures. Amphibians and reptiles are generally, but not always inactive during cold or dry weather. For instance, Semlitsch (1983, 1985) noted that mole salamanders (*Ambystoma* sp.) in South Carolina bred during the coldest but not necessarily the wettest months. He felt that most animals moved to breeding ponds at this time to allow sufficient time for larval development prior to pond drying (Semlitsch 1987). Such may not explain winter/early spring breeding in *N. perstriatus* because the breeding period is extended (Bishop 1947) and larvae have been found from April through December (Christman and Means 1978). The larval period is unknown, but its duration is critical to successful reproduction in temporary sandhills ponds.

Individuals moving at times of unusually cold and dry weather may be searching for more favorable retreats or escaping adverse conditions. If the onset of migration (sensu Semlitsch 1985) commenced during unusually adverse conditions, and the unfavorable conditions extended for a long period of time, the population could be vulnerable to local extinction via mortality or emigration. Prolonged drought brought about the local extinction, via emigration, of the resident *Seminatrix* population.

Movement Patterns and Orientation

Because of the small size of Breezeway Pond, it is difficult to ascribe directed movements of individuals as migrating to, or originating from, a specific habitat type. Because the pond was located in an ecotone, an animal captured at buckets facing the interface between sandhills and xeric hammock could move in either direction once beyond the fence. Likewise, an animal originating from one habi-

tat type could be misclassified if it moved a relatively short distance and fell into a bucket facing a different habitat type. The open field was also rather small and, although we did not feel comfortable assigning buckets 4-6 to sandhills or xeric hammock, it is likely that animals exiting or entering the pond through these buckets came from or went to one or the other habitat.

Given these qualifications, adult *Gastrophryne* did not exhibit habitat preferences, although juveniles left the pond primarily toward sandhills. *Gastrophryne* are commonly recorded in sandhills (Carr 1940, Campbell and Christman 1982, Mushinsky 1985) and have been found in sandhills > 100 m from the nearest water source (Franz 1986, Dodd pers. obs.). Xeric hammock or sandhills apparently provide narrow-mouthed toads suitable cover and resources away from the breeding pond, but why juvenile *Gastrophryne* would move toward sandhills is unknown.

Striped newts are most commonly found in flatwoods ponds in pine-palmetto habitats (Christman and Means 1978) as well as ponds in sandhills and scrub areas (Campbell and Christman 1982). To what extent they use sandhills habitats away from ponds is unknown. Carr (1940, reported as *N. v. symmetrica*) recorded efts in high and mesophytic hammocks in light, porous soil. However, striped newts at Breezeway Pond moved toward sandhills or meadow rather than hammock. Migration distances of striped newts are unknown although displaced *N. viridescens* can move 400 m through deciduous forest to return to a resident pond (Gill 1979). *N. perstriatus* probably can travel similar distances in its migrations.

Management Implications

The Florida sandhills are undergoing extensive habitat alteration because of rapid human population growth

and associated development. In the late 1970's, Auffenberg and Franz (1982) estimated that 70.6% of the sand pine-scrub oak, 57% of the long-leaf pine, and 37.7% of the xeric hammock communities had been destroyed by forest plantation agriculture and urbanization. In Putnam County, the site of our study, > 50% of the land area originally supporting such communities no longer does so. With projected human population increases of more than 300% between 1972 and 2000 (Auffenberg and Franz 1982), there has been increasing concern for the loss of sandhills habitats in northern and central Florida. Extensive loss of habitat is occurring in other portions of the state and Southeast, such that only 14% of the long-leaf pine (*Pinus palustris*) forests remain from estimates of over 70 million acres that once comprised this community (Means and Grow 1985).

Because of habitat loss, amphibian and reptile populations dependent upon sandhills probably are declining. Many of the amphibians, such as the Florida gopher frog, *Rana areolata aesopus*, and the striped newt, *N. perstriatus*, are considered endangered, threatened, or rare (Fogarty 1978, Christman and Means 1978), yet there are few data on their life histories or population dynamics.

The paucity of information on species composition and population dynamics of amphibians and reptiles that use temporary ponds in xeric habitat masks the probable importance of such habitats. Variation in annual habitat use, both intraspecifically and inter-specifically, appears to be considerable. Long-term ecological studies of the herpetofaunal community are needed to understand the magnitude of such variation and its potential significance.

Information on the biology of the species comprising the sandhills herpetofaunal community could be important in planning for the management of sandhills ecosystems by State and Federal agencies. For instance, Florida Statutes Section

373.414 required Water Management Districts to adopt rules to establish specific permitting-criteria for small isolated wetlands, including size thresholds below which impacts on fish and wildlife habitats would not be considered. When these rules were adopted, almost no data were available on herpetofaunal communities on which to make recommendations for size threshold considerations. Lack of information led, in part, to variation among regulations adopted by the different Water Management Districts.

There is considerable interest among Florida biologists, conservationists, and land use planners in the concept of wildlife corridors to maintain biotic diversity (Harris 1985). Unfortunately, most discussions have centered on riparian habitats. The lack of data on sandhills habitat use, especially by candidate endangered or threatened species, could hamper the long-term survival of such species. Many sandhills species are likely dependent on small isolated wetlands for at least a portion of their life cycle. By focusing on riparian habitats, planners may be overlooking the importance of upland habitats and their associated small wetlands to the maintenance of biotic diversity.

The following are the most important implications of our study for the conservation and management of small isolated wetlands and their associated herpetofaunal communities in "high pine" xeric habitats in northern and central Florida. These should be kept in mind when evaluating impacts of habitat loss and planning assessment studies.

1. Many species use these habitats: some are permanent residents, some are migrants, and some wander through the area on an irregular basis. All pond-breeding species live in surrounding terrestrial habitats during the non-breeding season. Thus,

the pond and a portion of the terrestrial habitat are both critical to species persistence.

2. Such habitats are used year-round despite seemingly unfavorable periods of drought and cold weather.
3. Species composition varies within a year: some species are found only in one season, some predominate at one time but are found commonly at other times, some are very rarely observed.
4. Reproductive output among species varies considerably: in one year spring breeders may be successful, in other years summer breeders may be successful, in some years both probably produce young, in other years neither may successfully reproduce. The longer that studies are conducted, the greater is the likelihood that multiple patterns will emerge.
5. Activity patterns change seasonally and annually probably in response to environmental cues, particularly rainfall, temperature, and hydroperiod.
6. To determine the total number of species using such wetlands, spring and early summer sampling produces the best results, but single season or even yearly sampling will not catch all species.
7. Quick surveys underestimate both numbers of species and individuals, as well as annual variation, and thus underestimate the importance of temporary isolated wetlands in sandhills.

8. To adequately understand complex communities, long-term studies are absolutely essential for management and conservation.

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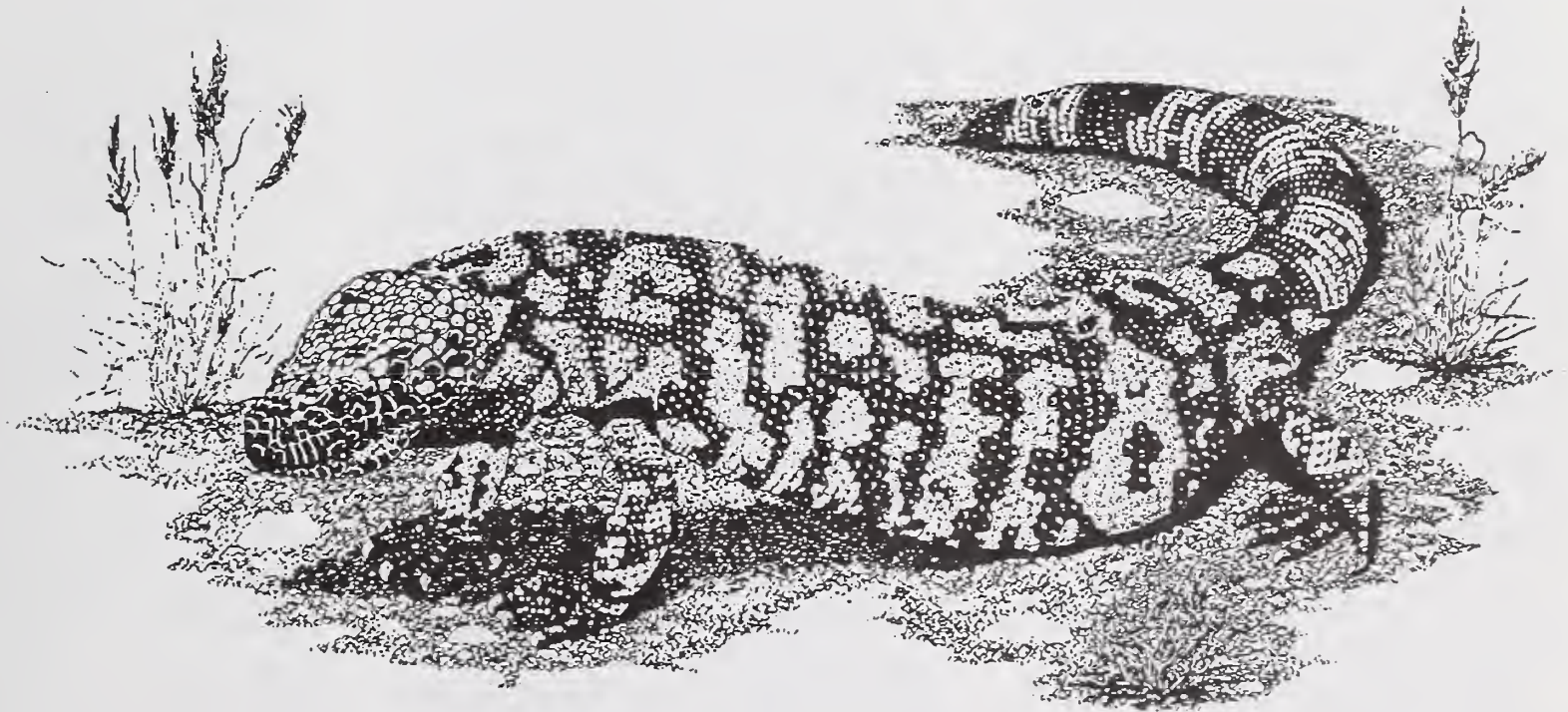
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Management of Amphibians, Reptiles, and Small Mammals in Xeric Pinelands of Peninsular Florida¹

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Xeric pinelands seem incongruent with reference to Florida, a state with annual rainfall that ranges from 50-65 in (19.6-25.6 cm). Nonetheless, the Florida peninsula contains thousands of acres of sandy soil derived from marine deposits dating to the Pleistocene (White 1970). Two distinct plant associations, longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) sandhill and sand pine scrub (*Pinus clausa*), have developed on these nutrient deficient and excessively well-drained soils. Significant areas of these plant associations occur at higher, albeit modest, elevations relative to the surrounding landscape. In fact, certain topographic features, e.g., the Lake Wales Ridge and the Marion Upland, were likely to have been true islands during interglacial periods while the remainder of Florida was covered by a shallow sea. Regardless of their exact origin, xeric pinelands support many relatively unusual species of amphibians, reptiles, and small mammals.

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Human population growth (3.3% per year) and development in Florida continues to encroach on upland habitats and particularly on xeric pinelands. Most of the habitat loss is to agricultural uses, principally citrus. Oddly, the state's excellent wetlands protection acts have forced development into the uplands. Thus, xeric pinelands and their narrowly adapted fauna and flora are increasingly threatened by area reduction, fragmentation and isolation.

It is our intent to discuss the management of these xeric pinelands in general and, more specifically, in the context of small preserves in an otherwise developed landscape. Management of xeric pinelands as ecosystems is yet in its infancy, and more detailed prescriptions for designated species are unproven. However, progress is being made (Cox et al. 1987) and improvement and revision of current thinking on management practices is anticipated. This paper summarizes selected literature on xeric pineland and the species associated with these communities to assess management practices. In addition, unpublished information has been used and identified in the text.

Preserve design efforts by us have been on behalf of developers responding to development orders prepared by governmental agencies. These designs are site specific in detail, but nonetheless point to general problems and solutions. Our approach has been to focus on provid-

Abstract.—The primary xeric pinelands of peninsular Florida are longleaf pine/turkey oak sandhills and sand pine scrub. Their management on public lands is largely confined to prescribed burning to maintain fire climax status of the vegetation. The regulation of large-scale developments on private land has stimulated interest in preserve design and management. The suite of techniques used to solve conflict between natural system preservation and development includes: (1) conservation set asides (preserves) on site; (2) habitat restoration; (3) purchase and dedication of off-site preserves; (4) species relocation; and (5) wildlife resource mitigation fund.

ing the area required to support minimum viable populations of "keystone" or otherwise critical animal species of a given xeric pineland. Once this area is settled on, management should focus on those species whose minimum area requirements are met, whereas no special efforts are expended on species with larger area requirements.

XERIC PINELAND HABITATS

Longleaf Pine/Turkey Oak Sandhills

The longleaf pine/turkey oak sandhill association (LLP/TO) was about 15% (2, 110, 256 ha) of the natural landscape of peninsular Florida in pre-Columbian times (fig. 1) (Auffenberg and Franz 1982). This xeric pineland occupies rolling topography of several ridge systems that run north-south, notably Trail Ridge, the Lake Wales Ridge, and the Brooksville Ridge; numerous lesser ridges and hills are identified by White (1970). These ridges consist of deep, well-drained soils of the Lakeland, Eustis, and Blanton associations (Beckenbach and Hammett 1962). Laessle (1942, 1958a) describes the LLP/TO plant association as a fire climax system dominated by longleaf pine; slash pine (*Pinus elliotti*) replaces longleaf pine in the community in south Florida. Turkey oak is a minor tree, but can achieve

co-dominance when fires are suppressed. The predominant understory plant is wiregrass, *Aristida stricta*; however, a rich assemblage of perennial herbs vary in prominence in concert with seasonal changes. Monk (1968) recognizes two additional phases of sandhill vegetation in north central Florida: (1) longleaf pine/sand post oak (*Quercus margaretta*) and (2) longleaf pine/southern red oak (*Quercus falcata*). A fourth phase, longleaf pine/scrub hickory (*Carya floridana*), occurs in the southern portion of the Lake Wales Ridge (Abrahamson et al. 1984). Veno (1976), Givens et al. (1984), and Abrahamson et al. (1984) provide quantitative data on LLP/TO community structure and dynamics. Myers (1985) suggests that longleaf pine/turkey oak and sand pine scrub associations are successional linked in some portions of their geographic ranges. Differences in physical/chemical features of soils of LLP/TO and SPS communities in the Ocala National Forest are not considered to be sufficient to explain the local dis-

tribution of the communities (Kalisz and Stone 1984).

Prior to settlement by European man, ground fires occurred in LLP/TO sandhills at intervals of 1-5 years. These relatively "cool" fires favor regeneration of longleaf pine, flowering by grasses and herbs, and suppress growth of woody plants (Myers 1985).

Sand Pine Scrub

Compared with the LLP/TO sandhill association, sand pine scrub (SPS) has less area (250,000 ha) and a far more limited distribution (fig. 1). Scrub is associated with old shorelines, lake margins, and stream courses where extremely well washed, nutrient deficient sands were deposited during Pleistocene times (Kurz 1942; Laessle 1958a, b, 1967). The most widespread soils supporting SPS are the St. Lucie, Lakewood, and Pomello associations (Beckenbach and Hammett 1962).

Sand pine scrub is a two-layered community. Sand pine (*Pinus clausa*) normally occurs as a relatively even-aged overstory species. The understory is comprised of 10-20 species of evergreen shrubs 1-5m in height. Four species of oaks comprise the bulk of the biomass, *Quercus geminata*, *Q. myrtifolia*, *Q. chapmanii*, and *Q. inopina*. Lesser numbers of other species including *Ceratiola ericoides*, *Lyonia ferruginea*, and *Osmanthus americanus* add to local diversity. Sand pine scrub is a fire climax community (Laessle 1958a, Abrahamson et al. 1984). In contrast with LLP/TO, SPS burns at intervals of 20-70 years; a combination of ground and crown fires destroys all the above-ground vegetation. Most of the woody plants, with the notable exception of the sand pine and *Ceratiola*, readily sprout from root crowns following fires. Laessle (1958a), Veno (1976), and Richardson (1977) provide data on plant community structure of scrubs. Recent quantitative studies

include those of Abrahamson et al. (1984) and Latham (1985).

Outstanding examples of SPS include the "Big Scrub," part of the Ocala National Forest, scrubs of the Lake Wales Ridge, e.g., the Archbold Biological Station, and stands along the Atlantic Coastal Ridge.

SMALL VERTEBRATE SPECIES ASSEMBLAGES

Longleaf Pine/Turkey Oak Sandhills

Amphibians and Reptiles

At least 47 species of herptiles, including 2 newts, 13 toads and frogs, 3 turtles, 10 lizards, 1 amphisbaenian, and 18 snakes, are reported to occur in LLP/TO habitats (table 1). Campbell and Christman (1982) list 5 categories of reptile and amphibian species that occur in LLP/TO and SPS: (1) characteristic (18 species); (2) associated with tortoise burrows (3 species); (3) frequent (8 species); (4) occasional (14 species); and (5) associated with aquatic habitats (21 species). Of the characteristic species, 7 are regarded as adapted to xeric conditions, 3 as sand swimmers, viz., *Neoseps reynoldsi*, *Eumeces egregius*, and *Tantilla relicta*, and the remainder (*Sceloporus woodi*, *Masticophis flagellum*, *Stilosoma extenuatum*, *Cnemidophorus sexlineatus*) to other physical features of the habitats.

The gopher tortoise (*Gopherus polyphemus*) is a terrestrial turtle that digs deep burrows in the well-drained sandhill soils (Auffenberg and Franz 1982). Stout (1981) and Eisenberg (1983) recognized the gopher tortoise was the keystone species in xeric pinelands. Some 80 species of animals may be classified as burrow commensals (Cox et al. 1987); however, the number of obligatory commensals is much smaller. Herptiles particularly associated with gopher tortoise burrows include *Rana*



Figure 1.—Potential geographic distribution of longleaf pine/turkey oak sandhill and sand pine scrub xeric pinelands in Florida. Light shading indicates the sandhills and darker shading indicates the scrub. These distributions are based on Davis (1980) and do not reflect minor sites of either community due to the scale of the illustration.

areolata, *Pituophis melanoleucus*, and *Drymarchon corais*.

The snake fauna of LLP/TO sandhills is species rich (≥ 18 species). This diversity includes large forms, e.g., *Drymarchon corais couperi* and *Crotalus adamanteus*, and small, specialized species like *Stilosoma extenuatum*. This latter ophiophagous species feeds largely on *Tantilla relict*a; *Tantilla*, in turn specialized on Tenebrionidae larvae (Mushinsky 1984).

Small Mammals

At least 19 species of small mammals with body masses less than 6.0 kg

may be anticipated in LLP/TO sandhills (table 2). Two are fossorial, *Scalopus aquaticus* and *Geomys pinetia*, 1 semi-fossorial, *P. polionotus*, and 2 occur in the surface litter, *Blarina carolinensis* and *Cryptotis parva*.

Arboreal species include *Sciurus carolinensis*, *S. niger*, *Glaucomys volans*, *P. gossypinus*, and *Ochrotomys nuttalli*. *Podomys floridanus* nests in the burrows of the gopher tortoise and the pocket gopher (Layne 1969); it may enlarge other openings in the soil to establish burrows independently of the gopher tortoise (R. E. Roberts, personal observation). *Dasypus novemcinctus* is the only exotic species of mammal that is clearly

established in the sandhill community.

Sand Pine Scrub

Amphibians and Reptiles

Campbell and Christman (1982) listed 64 species of reptiles and amphibians that may be found in LLP/TO sandhills and SPS. Pitfall trapping in six different even-aged stands of SPS on the Ocala National Forest by Christman et al. (unpublished manuscript and personal communication) revealed 27 species (table 1). Of 1,624 individuals

Table 1.—Herpetofauna trapped or observed within the xeric pinelands of peninsula Florida. Standard herp arrays were used in each study to sample for a period of at least one year.

Species	Long leaf pine/ turkey oak			Sand pine scrub	Species	Long leaf pine/ turkey oak			Sand pine scrub
	Campbell & Christman 1982	Mushinsky 1985	Stout et al. unpubl.			Campbell & Christman 1982	Mushinsky 1985	Stout et al. unpubl.	
<i>Notophthalmus viridescens</i>	—	—	x	—	<i>Scincella lateralis</i>	x	x	x	x
<i>N. perstriatus</i>	—	—	—	x	<i>Eumeces inexpectatus</i>	x	x	x	x
<i>Scaphiopus holbrookii</i>	x	x	x	x	<i>E. egregius lividus</i>	—	—	x	x
<i>Bufo terrestris</i>	x	x	x	x	<i>E. egregius onocrepis</i>	x	—	x	x
<i>Bufo quercicus</i>	x	x	x	x	<i>Neoseps reynoldsi</i>	x	—	x	x
<i>Eleutherodactylus planirostris</i>	—	x	—	—	<i>Rhineura floridana</i>	x	—	x	x
<i>Hyla femoralis</i>	x	—	x	x	<i>Nerodia fasciata</i>	—	x	—	—
<i>Hyla gratiosa</i>	x	—	x	—	<i>Thamnophis sauritus</i>	—	x	—	—
<i>Hyla squirella</i>	—	—	x	—	<i>Rhadinaea flavilata</i>	—	x	—	—
<i>Hyla cinerea</i>	—	x	—	—	<i>Diadophis punctatus</i>	x	x	—	—
<i>Acris gryllus</i>	—	—	x	—	<i>Farancia abacura</i>	—	x	—	—
<i>Rana grylio</i>	—	x	—	—	<i>Coluber constrictor</i>	x	x	x	x
<i>Rana areolata</i>	x	x	x	x	<i>Masticophis flagellum</i>	x	—	—	x
<i>Rana utricularia</i>	—	x	—	—	<i>Opheodrys aestivus</i>	x	—	—	—
<i>Gastrophryne carolinensis</i>	x	x	x	x	<i>Drymarchon corais</i>	—	x	x	—
<i>Kinosternon bauri</i>	—	x	x	—	<i>Elaphe guttata</i>	—	—	—	x
<i>Terrapene carolina bauri</i>	—	—	x	—	<i>Pituophis melanoleucus</i>	x	x	x	—
<i>Gopherus polyphemus</i>	x	x	x	x	<i>Lampropeltis triangulum</i>	x	—	x	x
<i>Anolis carolinensis</i>	x	x	x	x	<i>Stilosoma extenuatum</i>	x	—	—	x
<i>Anolis sagrei</i>	—	—	x	—	<i>Cemophora coccinea</i>	x	x	x	x
<i>Sceloporus undulatus</i>	—	—	x	—	<i>Tantilla relict</i> a	x	x	x	x
<i>Sceloporus woodi</i>	x	—	x	x	<i>Heterodon platyrhinos</i>	x	x	x	x
<i>Ophisaurus compressus</i>	x	—	—	—	<i>Heterodon simus</i>	—	—	x	—
<i>Cnemidophorus sexlineatus</i>	x	x	x	x	<i>Micrurus fulvius fulvius</i>	x	—	x	x
					<i>Sistrurus miliaris</i>	x	—	—	x
					<i>Crotalus adamanteus</i>	—	x	—	—
					Totals	29	27	33	27

trapped, the common species were *Bufo terrestris* (n=332), *Cnemidophorus sexlineatus* (n=329), and *Sceloporus woodi* (n=216); five species were represented by single captures. Christman et al. concluded that the herpetofaunal diversity declined with increasing age of SPS stands.

Gopherus polyphemus is the key-stone species in SPS but is less common there than in LLP/TO (Auffenberg and Franz 1982). Many, if not most, of the burrow commensals are common in SPS (Cox et al. 1987). *Podomys floridanus* is an example.

Small Mammals

Fourteen species of small mammals commonly inhabit SPS (table 2). *Pod-*

omys floridanus is a predictable member of the assemblage throughout the range of scrubs in peninsular Florida (Layne 1978). Three subspecies of *Peromyscus polionotus* occur in scrubs of the interior and east coast portions of the peninsula. Common small mammals in central peninsular Florida scrubs include *Podomys floridanus*, *Peromyscus gossypinus*, *Ochrotomys nuttalli*, and *Glaucmys volans* (Swindell 1987). *Podomys floridanus* is the predominate small mammal in scrubs of southeast Florida (Richardson et al. 1986).

Limited data suggest *Spilogale putorius* is a major predator on small mammals in scrubs with lesser roles played by *Mephitis mephitis* and *Mustela frenata* (Stout and Roberts, personal observations).

ENDANGERED AND THREATENED SPECIES

Ten species of amphibians, reptiles, and small mammals associated with xeric pineland are currently listed as having some level of threatened, endangered, or sensitive status by either the state of Florida or the Department of Interior (table 3). The extensive overlap in species composition between the two pineland communities results from the high number of species common to both types. The Endangered Species Act charges federal agencies with the responsibility to manage federally listed species on federally owned lands. At the state level, preservation of these listed species is of major concern when they occur on parcels of land scheduled for large-scale development. Preserve design and management practices for these species have largely evolved on an *ad hoc* basis without adequate time for an evaluation of the management or the long-term implications for the species.

MANAGEMENT OF XERIC PINELANDS ON PUBLIC LANDS

Of three national forests in Florida, only the Ocala National Forest is located in the peninsula. It totals 153,846 ha of which 85,020 ha are SPS and 18,219 ha LLP/TO. The National Forest Management Act (1976) and pursuant regulations (36 CFR 219) require that each forest be managed to maintain well-distributed and viable populations of wildlife species, including species that are endangered or threatened (Norse et al. 1986).

Silvicultural systems differ between the two pineland communities. On the Ocala National Forest sand pine scrub is routinely harvested in patchy clearcuts that range from 16-24 ha in area. Scrub understory vegetation is allowed to regenerate naturally; however, sand pine is seeded following site preparation

Table 2.—Small mammal community structure in sandhill and sand pine scrub plant associations of peninsular Florida. The upper limit of body mass of small mammals was arbitrarily set at 6.0 kg.

Mammal Species	Longleaf pine/turkey oak ^{1,2,3}	Sand pine scrub ⁴
<i>Didelphis virginiana</i>	x	x
<i>Cryptotis parva</i>	x	—
<i>Blarina carolinensis</i>	x	x
<i>Scalopus aquaticus</i>	x	—
<i>Dasypus novemcinctus</i>	x	x
<i>Sylvilagus floridanus</i>	x	x
<i>Sciurus carolinensis</i>	x	x
<i>Sciurus niger</i>	x	—
<i>Glaucmys volans</i>	x	x
<i>Geomys pinetis</i>	x	—
<i>Peromyscus polionotus</i>	x	x
<i>Peromyscus gossypinus</i>	x	x
<i>Podomys floridanus</i>	x	x
<i>Ochrotomys nuttalli</i>	x	x
<i>Sigmodon hispidus</i>	x	x
<i>Urocyon cinereoargenteus</i>	x	—
<i>Procyon lotor</i>	x	x
<i>Mustela frenata</i>	?	x
<i>Spilogale putorius</i>	x	x
<i>Mephitis mephitis</i>	x	—
No. Species	19	14

¹Stout et al., unpublished

²Arata 1959

³Humphrey et al. 1985

⁴Stout 1982

by a single roller chopping. The harvest rotation length is about 50 years. In contrast, LLP/TO is ostensibly managed on a 80-100 year rotation and shelterwood cutting favors natural regeneration of the longleaf pine (Don Bethancourt, personal communication). In practice, harvesting of longleaf pine may occur in 60 years.

Effectiveness of ecosystem management in the SPS community will be judged by the response of designated indicator species, such as gopher tortoises and scrub jays (*Aphelocoma coerulescens*) (table 3). The gopher tortoise is also a designated indicator species for the LLP/TO community. The significance of the gopher tortoise as a keystone species was emphasized in 1986 when harvesting of the species on national forests in Florida was made illegal through an agreement between the U.S. Forest Service and the Florida Game and Fresh Water Fish Commission. Other species-specific management practices involving amphibians, reptiles, or small mammals have not

been deemed necessary to carry out on the Ocala National Forest (Don Bethancourt, personal communication). In fact, the impact of timber harvesting on small vertebrates of LLP/TO and SPS communities is simply not known.

Public lands in Florida supporting xeric pinelands include, but are not limited to, state forests and state parks. State forests with large acreages of LLP/TO, e.g., the Withlacoochee State Forest, are managed at the ecosystem level. Prescribed burning is done every 3-8 years and future timber sales will follow a rotation length of 80-120 years; currently rotation lengths are about 60 years and are not regarded as favorably for endemic wildlife. Wildlife management areas overlap the state forest holdings and are managed for sustained yields of wildlife by the Florida Game and Fresh Water Fish Commission based on a memorandum of understanding between agencies (Cathy Ryan, personal communication).

State parks are managed by the Division of Recreation and Parks of the Florida Department of Natural Resources (FDNR). An ecosystem approach is taken in the restoration and management of xeric pinelands on state park lands (Jim Stevenson, personal communication). Prescribed burning has been used since 1969 to control hardwood invasion of LLP/TO stands and to stimulate growth and flowering of grasses and herbs. Burning in spring and early summer appears to best duplicate the historic timing of lightning initiated fires in xeric pinelands. The impact of these management practices on the plant community has been documented (Davis 1984); the response of reptiles, amphibians, and small mammals is currently under study (Stout et al. unpublished). Generally, mature stands of SPS have not been burned until recently, due to the unpredictable behavior of fire in the community; however, a prescription for burning this fuel type has been written and tested on private land and state parks (Doran et al. 1987). Early recovery stages of SPS appear to support the greatest diversity of reptiles and amphibians. However, as canopy closure occurs in SPS, ground cover diminishes and habitat quality for gopher tortoises declines (Cox et al. 1987). In contrast, similar numbers of *Podomys* have been observed in early (R. E. Roberts, unpublished data, J. Dickinson State Park); intermediate (Stout 1982); and old growth SPS (James N. Layne, unpublished data, Archbold Biological Station).

State parks, reserves, and preserves appear to be ideal lands to explore species-specific management measures for herptiles and small mammals. For example, sand swimming herptiles (Smith 1982) require openings that are relatively root free in LLP/TO and SPS habitats. The natural occurrence of such openings may have been due to "hot" spots associated with the combustion of high fuel loads, e.g., fallen trees (Ron Myers, personal communication).

Table 3.—Endangered and potentially endangered amphibians, reptiles, and small mammals (Wood 1987) inhabiting xeric pinelands of peninsular Florida.

Species group	Xeric pineland		Designated status ¹	
	LLP/TO	SPS	FGWFC ²	USFWS ³
Amphibians and Reptiles				
<i>Drymarchon corais couperi</i>	X	X	T	T
<i>Eumeces egregius lividus</i>	X	X	T	T
<i>Gopherus polyphemus</i>	X	X	SSC	UR2
<i>Neoseps reynoldsi</i>	X	X	T	T
<i>Pituophis melanoleucus mugitus</i>	X	X	SSC	UR2
<i>Rana areolata</i>	X	X	SSC	UR2
<i>Stilosoma extenuatum</i>	X	X	T	UR2
Mammals				
<i>Geomys pinetis goffi</i>	X	—	E	UR3
<i>Podomys floridanus</i>	X	X	SSC	UR2
<i>Sciurus niger shermani</i>	X	—	SSC	UR2

¹E= Endangered; T=Threatened; SSC= Species of Special Concern; UR2= Under review for listing, but substantial evidence of biological vulnerability and/or threat is lacking; UR3 = Still formally under review for listing, but no longer being considered for listing due to existing pervasive evidence of extinction.

²Florida Game and Fresh Water Fish Commission

³United States Fish and Wildlife Service

Concentration of natural fuels prior to prescription burns in SPS would offer a means to create microhabitat conditions favorable for the sand swimmers.

MANAGEMENT OF XERIC PINELAND ON PRIVATE LAND

Development of Regional Impact

Concern with management of amphibians, reptiles, and small mammals on private lands in Florida derives from state and federal protection of endangered species and the development guidelines promulgated during the Development of Regional Impact (DRI) process. "The Florida Environmental Land and Water Management Act of 1972" (Chapter 380, Florida Statutes) defines developments of regional impact in Section 380.06(1), Florida Statutes, as "...any development which, because of its character, magnitude, or location, would have a substantial effect upon the health, safety, or welfare of citizens of more than one county (Anonymous 1976)." Large scale development projects in peninsular Florida commonly involve hundreds to several thousand acres of relatively natural landscape. The DRI process requires bona fide studies of wildlife populations and their associated habitats; emphasis is placed on listed species. Developers must prepare viable management strategies to accommodate wildlife resources dependent upon their lands (Cox et al. 1987; Richardson et al. 1986).

Management strategies of developers with xeric pinelands generally follow one of two somewhat overlapping approaches to preserve habitat and/or species values: (1) conservation set asides or (2) mitigation. Conservation set asides are, in principle, the preferred solution. In practice some habitat is dedicated in perpetuity as a nature preserve; preserve design currently is a somewhat *ad hoc* process and will be discussed more

completely in a subsequent section of this paper. Very high land values may dictate mitigation rather than on site preservation of habitat.

Mitigation may take many forms to compensate for development of xeric pinelands. Restoration of degraded land (Humphrey et al. 1985), not necessarily xeric pinelands, is one method. Another tactic is to purchase comparable land or some other type of land of equivalent natural value elsewhere and dedicate it to preservation. A formal process for accomplishing this option is presently under study by the Florida Game and Fresh Water Fish Commission.

Preservation of habitat is the basic purpose of conservation set asides and mitigations. The value of these efforts depends on the proximity to larger, undeveloped tracts of land, travel corridors, area of preserves, and future management options.

Another form of mitigation is the relocation of sensitive species from tracts of land to be developed to land dedicated to purposes that are consistent with the long-term survival of the relocated species. In Florida, the gopher tortoise has been the focus of numerous relocation efforts. Diemer (1984) discussed the advantages and disadvantages of relocation of gopher tortoises as a species management strategy. Formal research on gopher tortoise relocation was recently reported (Proced. Gopher Tortoise Relocation Symp., 27 June 1987, Gainesville, FL, in press). The Florida Game and Fresh Water Fish Commission regulates relocations by a permit system based on a standardized relocation protocol.

Preserve Design

Preserve design is an evolving and controversial area of conservation biology (Diamond 1975, 1978; Gilbert 1980; Higgs 1981; Margules 1982; Pickett and Thompson 1978; Pyle 1980; Soule and Simberloff 1986). Large preserves encompassing a mo-

saic of xeric pinelands, mesic forests, and seasonal and permanent wetlands would perhaps offer the ideal landscape unit for long-term preservation of amphibians, reptiles, and small mammals in peninsular Florida. Because preserves on private lands must be justified and dedicated through the DRI process, economics dictates preserve units of minimal size. Rarely do we have the opportunity to cluster or juxtapose these small units to take advantage of the so called "rescue effect" (Brown and Kodric-Brown 1977).

In practice, conservation set asides tend not only to be small in acreage but also only of one habitat type. The latter presents a dilemma for species whose requirements often include two or more contrasting habitats. For example, the gopher frog lives in tortoise burrows in LLP/TO sandhills during late spring, summer and early fall and migrates to temporary wet season depressions to breed in winter and early spring (Moler and Franz 1987). Thus a mosaic of upland-wetland habitats in close proximity are essential to maintain viable populations of this species. Other species such as the indigo snake have home range requirements that include 122-202 ha of several upland-wetland habitat types (Moler 1985; Moler unpublished data). It is obvious that large landscape units are necessary to preserve viable populations of these animals.

We have prepared a detailed preserve design for a SPS community within the city of Boca Raton, Florida (Richardson et al. 1986; Stout et al. 1987; manuscript in preparation). The approach taken anticipated Soule and Simberloff (1986) and recommended the area of the preserve be sufficient to support a minimum viable population (Franklin 1980) of gopher tortoises because of their status as the keystone species. Although biologically reasonable, this basis for determining preserve size is often economically unrealistic from the view point of the private land-

owner. A consortium of public land-owners would, however, permit the purchase and long-term management of the preserve as recommended.

Cox et al. (1987) offer guidelines for the design of preserves on private lands to maintain gopher tortoise populations. They employed the computer simulation model POPDYN (Perez-Trejo and Samson manuscript) to determine population viability based on different initial sizes. Populations of 40-50 individuals were found to be likely ($\geq 90\%$) to persist 200 years. Based on existing literature on home range requirements, Cox et al. (1987) recommended a minimum preserve of 10-

20 ha, depending on habitat quality, to support 40-50 tortoises.

Another approach to determining the area of a preserve employs "incidence functions" (Diamond 1978). Incidence functions are species specific and derived from data sets which reveal the fraction of plots (discrete habitats) of different areas that actually support the species. It is a matter of judgement as to the probability of occurrence, e.g. 0.5 as opposed to 0.7, that would set a lower limit to area for an acceptable preserve. Data sets useful for evaluating this approach with respect to amphibians, reptiles, and small mammals in xeric pinelands are pres-

ently lacking. Table 4 provides data we have gathered on area of discrete habitats and the presence or absence of gopher tortoises and Florida mice. It is apparent that tortoises are less area sensitive than Florida mice and that Florida mice are patchy in occurrence in LLP/TO, perhaps only secondarily related to area.

Incidence functions do not necessarily reveal the minimum area required to support minimum viable populations (Franklin 1980). We believe preserve area should be based on providing this requirement, particularly when preserves are isolated relative to average dispersal distances of keystone species. However, clusters of preserves within dispersal distances of keystone species may be of less area per preserve due to a high likelihood of reinvasion from nearby populations following local population extirpations (Noss and Harris 1986).

Table 4.—Incidence of *Gopherus polyphemus* a keystone species, and *Podomys floridanus* in xeric pinelands of peninsular Florida. Presence (+) or absence (-) is indicated. Study sites are ranked according to area within the xeric pinelands. Quantitative sampling of the 12 LLP/TO study sites consisted of 5 days of live-trapping and observation at intervals of 3 months over a period of 18 months (1986-1988). Study sites in SPS were sampled by live-trapping and observation a minimum of 3 consecutive days, often in the same season of consecutive years (Stout et al. unpublished).

Study sites	Area (ha)	Incidence of species in xeric pineland			
		LLP/TO		SPS	
		<i>Gopherus</i>	<i>Podomys</i>	<i>Gopherus</i>	<i>Podomys</i>
Lake Mary	1.2	+	—		
Morningside Nature Center	2.0	+	—		
San Felasco	4.1	+	—		
Spruce Creek	4.1	+	—		
Orange City	5.6	+	—		
Bok Tower	9.3	+	—		
Wekiwa Springs	9.7	+	+		
Suwannee River	10.1	+	+		
O'Lena	10.5	+	+		
J. Butterfield Brooks	15.8	+	+		
Starkey Well Field	16.2	+	—		
Sandhill Boy Scout Camp	16.2	+	—		
Interlachen	21.8	+	—		
Yamato Plaza	2.8			+	—
Yamato Scrub, B	3.2			+	+
Quantum Park, A	4.4			+	+
Quantum Park, B	4.4			+	+
Quantum Park, C	4.8			+	+
Yamato Scrub, A	8.5			+	+
Summit Place	10.5			+	—
Potomac Road	17.8			+	+
Cedar Grove	21.5			+	+
J. Dickinson	256.2			+	+

Management of Preserves in Xeric Pinelands

The future viability of preserves depends largely on their ownership after development of the surrounding landscape. It is unlikely that homeowners associations will assume the cost of management if preserves remain as a part of the overall development's "commons." Public ownership is an alternative and might rest with a city, county, or state. Local governments seem more appropriate; however, funds and expertise to manage may be lacking. One preserve in south Florida is designed to border a city park, thus allowing its maintenance and/or management costs to be assumed over time as part of the existing park system (Richardson, personal observation). Regardless of the ownership, a commitment to long-term management must be achieved if a preserve is to retain natural values.

Management options for nature preserves range from a decision 1) to

do nothing and let nature take its course; 2) to manage for maintenance of a viable ecosystem, which implies the natural biota, including amphibians, reptiles, and small mammals, will be present in proportion to their normal abundance; or 3) to focus management on the needs of one or more species. White and Bratton (1980) have exposed the folly of the first management option. The decision to emphasize ecosystem or species management depends on the entity responsible for management, type of preserve, management objectives, area of the preserve, nature of the surrounding lands, relative overall or regional rarity of particular species, and the resources available for management.

Management objectives of any preserve should focus on: 1) maintenance of normal ecosystem processes; 2) conservation of soil; 3) maintenance or restoration of normal hydrologic conditions; 4) prevention of establishment of exotic species; 5) and prevention of human encroachment (e.g., dumping, ATVs, etc.) Beyond these generalities, management of preserves is an idiosyncratic process that may concern endemic species, genetics of inbred populations, or restoration of periodic wild fires.

Xeric pinelands of peninsular Florida depend on periodic fires to maintain their structure and function (Laessle 1958a; Abrahamson 1984). Thus a burning program is essential in the management of LLP/TO or SPS preserves. Spring or early summer prescribed burns are routinely used to maintain LLP/TO communities on state parks. Doran et al. (1987) have documented prescribed burns of SPS preserves in an urban setting based on rather esoteric fire models developed by the U.S. Forest Service. Gopher tortoises respond favorably to the burns (Stout et al. 1988). A mosaic of recovery stages in SPS may favor beta diversity of herptiles and small mammals. Mushinsky (1985) has carefully documented the response of the herpetofauna to a vari-

ety of burning schedules in LLP/TO. Diversity and abundance of amphibians and reptiles was increased on experimental plots relative to unburned controls. Re-establishment of the pine overstory may be necessary to produce needle cast for carrying fire (Landers and Speake 1980).

Management of conservation set asides and/or easements may focus on particular species or combinations of species. The smaller the preserve the more likely that a reduced suite of species will be present (Richardson et al. 1986). Given that a fixed area is available for management, major efforts to enhance or maintain habitat should target those species that can maintain viable populations within the preserve (Shaffer 1986). A species whose minimum area requirements for a minimum viable population exceeds the preserve area should not be of major concern (Shaffer and Samson 1985); nonetheless, such species can benefit from the preserves if travel corridors exist (Harris 1984).

DISCUSSION

Xeric pinelands of peninsular Florida support a species-rich assemblage of reptiles, amphibians, and small mammals. Growth and development continues to diminish LLP/TO and SPS habitats to the detriment of the associated biota. Land in public ownership, e.g. state parks and forests, national forests, and private holdings, e.g., the Archbold Biological Station, and institutional lands such as the Ordway and Swisher Preserves, jointly owned and managed by the University of Florida and The Nature Conservancy, will be increasingly valuable as other xeric pinelands are converted to land uses not favorable to the biota. Thus, management of these xeric pinelands will become more important in the future. At present management is largely limited to prescribed burns to maintain what were historically fire

climax communities. Thus, fire management is tantamount to small vertebrate management.

In the future as air quality standards are modified, prescribed burning, particularly in or near urbanized areas, will be restricted or eliminated as a management option. Alternative means of habitat manipulation need to be developed, particularly for SPS.

Basic information on the life history of many amphibians, reptiles, and small mammals of xeric pinelands is lacking. The Nongame Wildlife Program of the Florida Game and Fresh Water Fish Commission has initiated and funded rather large scale studies of SPS and LLP/TO communities. These studies are at the community level and largely observational. Management needs of individual species may be derived only secondarily from this research. Studies that focus on particular species will ultimately lead to more refined habitat management guidelines. The report by Cox et al. (1987) will likely serve as a model for the preparation of habitat protection guidelines; management follows protection (White and Bratton 1980).

Management alternatives at the ecosystem and species level are needed now for xeric pinelands on private lands undergoing development. Regulation of development in these habitats as currently practiced will result in a patchwork of small, isolated nature preserves. Preservation of natural habitat in a developed landscape is, of course, desirable. However, several problems remain: (1) who will own the preserves, (2) how will a management plan be prepared, and (3) who will be responsible for management? Even another decade of rapid growth in peninsular Florida may result in a few hundred nature preserves, which will not necessarily be restricted to xeric pineland habitat. Ignoring the question of ownership, no public land management agency is currently capable of assuming the charge of managing these preserves. Lack of manage-

ment, e.g., failure to conduct prescribed burning, will allow successional changes to occur to the detriment of many small vertebrates narrowly adapted to xeric pinelands. Loss of habitat and species values originally used by jurisdictional agencies to secure preserve set asides provides a potential basis for private land owners to request development rights on the land. This action would defeat the entire purpose of having conservation set asides.

An alternative to on site habitat protection is offered by Cox et al. (1987) in regard to preserving habitat for the gopher tortoise. The alternative, a Wildlife Resource Mitigation Fund (WRMF), allows a developer to contribute money to the fund to mitigate losses of valuable wildlife habitat on lands being developed. The collective monies of several development projects would allow an independent group such as the Trust For Public Lands to assist in the purchase of commensurate lands to expand an existing public park, preserve or forest. Management is more likely to be applied to these lands and ultimately the resources are better served by the public agencies.

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Distribution and Habitat Associations of Herpetofauna in Arizona: Comparisons by Habitat Type¹

K. Bruce Jones²

With the passage of the Federal Land Policy and Management Act in 1976, the Bureau of Land Management (BLM) was mandated to keep an inventory of resources on public lands. Information collected during inventories or surveys was then to be used to identify issues for land use planning and opportunities for land management. The BLM made a decision to collect data on all major wildlife groups and their habitats.

Early in the development of its inventory program, the BLM recognized a need to devise a strategy that would compare animal distributions and abundance to habitats. This strategy was important since the BLM manages wildlife habitats and not wildlife populations.

In 1977 the BLM initiated inventories of wildlife resources on public lands. At that time, considerable information was already available on game species. However, data on nongame species were mostly lacking. As a result, priority was given to collecting data on nongame species and their habitats.

Amphibians and reptiles are important members of the nongame fauna. They use a wide range of habi-

tats and are often good indicators of habitat conditions (Jones 1981a). Therefore, in order to obtain information on these animals, principally for land-use planning, the BLM conducted extensive inventories of amphibians and reptiles by habitat type. This inventory included a scheme whereby associations between amphibians and reptiles and certain microhabitats could be determined. The inventory, conducted between 1977 and 1981, was one of the most comprehensive surveys of herpetological communities ever conducted in North America (27,885 array-nights in 16 habitat types over a five-year period). It also represents the first large-scale effort to quantitatively compare herpetofaunas associated with ecosystems. This paper reports the results of these surveys, including species distributions and associations with microhabitats and habitat types (plant communities).

STUDY AREA

The study area consisted of approximately 3,441,296 ha (8.5 million acres) of public lands located in central, west-central, southwestern, and northwestern Arizona (fig. 1). Sixteen different habitat types were delineated within this area, primarily from an existing map of vegetation associations (Brown et al. 1979). Field reconnaissance allowed more local associations to be recognized within

Abstract.—Between 1977 and 1981, the Bureau of Land Management conducted extensive surveys of Arizona's herpetofauna in 16 different habitat types on approximately 8.5 million acres of public lands. This paper describes results of one of the most extensive surveys ever conducted on amphibian and reptile communities in North America.

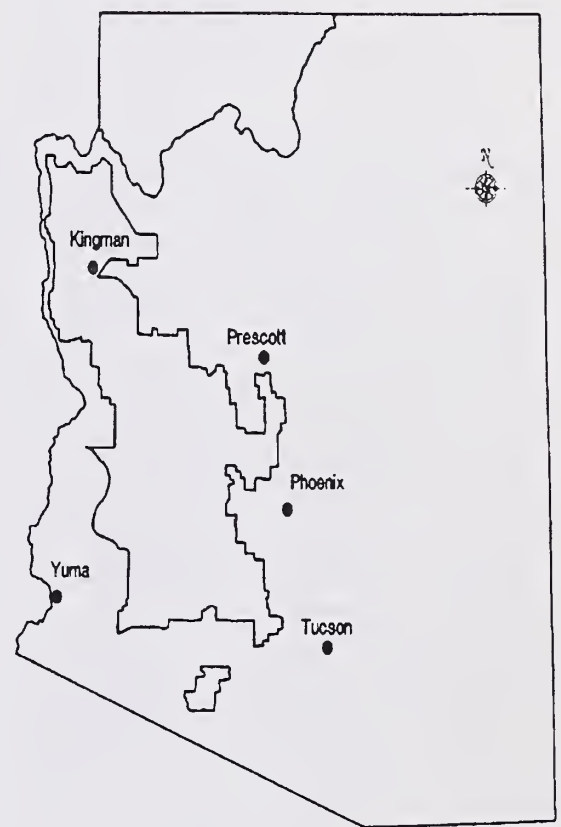


Figure 1.—The study area.

those presented by Brown et al. (1979). For example, because of the scale of their map, Brown et al. (1979) failed to recognize several small, relict stands of chaparral woodland, although Brown (1978) had noted the presence of chaparral woodland vegetation at several small sites (see Jones et al. 1985 for the importance of small woodland stands to certain herpetofauna). Therefore, the habitat type map used to allocate samples in this study drew upon the Brown (1978) and Brown et al. (1979) maps,

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and results of field reconnaissance. For detailed descriptions of these habitat types see Jones (1981b) and Buse (1981).

SAMPLING METHODS

Amphibian and reptile distribution and abundance by habitat type were determined by on-the-ground sampling efforts between October, 1977, and July, 1981. Samples were obtained by three methods. The most extensive sampling was accomplished with a pit-fall trapping method (array) consisting of a series

of 18.3 l (5 gal) plastic containers buried in the ground and connected by 0.41 m (8 inches) high aluminum drift fence; one trap was located in the center with three evenly dispersed (120°) peripheral traps 7.14 m (25 ft) from the center (Jones 1981a, Jones 1986). This modified array method was designed specifically for sampling amphibians and reptiles in desert habitats (see Jones 1986 for a comparison of this procedure with the original array trapping scheme designed by Christman and Campbell 1982). A total of 183 arrays were used to sample 16 different habitat types (see table 1 for sum-

mary of sampling effort in each habitat type). Arrays were placed so that microhabitat variability within each habitat type was sampled. The number of arrays used to sample habitat types was partially influenced by the size of habitats; generally, more extensive habitats received proportionally larger samples. However, certain habitats (e.g., riparian) were known to be great sources of diversity within desert regions; therefore, priority was given to obtaining larger samples within these habitats. Once placed into the ground, arrays were continuously open for a minimum of 60 days. Some arrays (60) were open for 9 months. Generally, samples were taken during the spring, summer, and fall. However, some arrays (17) were open only during spring months and others only in the fall (12). The opening of new arrays at different locations, and the closing of other arrays, were often dictated by BLM's predetermined resource planning schedule.

Since some amphibians and many snakes could not be effectively sampled by pit-fall traps, it was necessary to use two other field techniques. Road riding, consisting of traveling roads from dusk to approximately 2300 h throughout delineated habitat types, was used to determine the occurrence of amphibians and medium and large snakes (see table 1 for sampling effort within each habitat type).

Time-constraint searches (Bury and Raphael 1983), consisting of walking along permanent and temporary water sources (natural and man-made) at night, were used to verify the presence of frogs and toads at waters within habitat types (see table 1 for sampling effort within each habitat type).

Finally, to get an idea of the known distribution of amphibians and reptiles within the study area, I obtained records from 7 museums known for their outstanding collections of amphibians and reptiles from the Southwest: the University of

Table 1.—Sampling effort in each habitat type.

# of arrays	# of trap nights	# of road riding road transects	# of field searches	Elevation range (m (ft.))	
Ponderosa Pine Woodland (PP)					
5	745	10	15	1677-2531	(5500-8300)
Pinyon-Juniper Woodland (PJ)					
9	945	14	20	1311-1921	(4300-6300)
Sagebrush (Great Basin Desert) (SB)					
3	270	12	12	1311-1830	(4300-6000)
Closed Chaparral (CC)					
18	2168	18	20	1250-2287	(4100-7500)
Open Chaparral (OC)					
13	1950	22	25	762-1311	(2500-4300)
Desert Grassland (DG)					
11	1155	15	14	1006-1525	(3300-5000)
Disclimax Desert Grassland (DD)					
3	300	11	10	884-1311	(2900-4300)
Mixed Broadleaf Riparian (MB)					
6	784	8	18	884-2287	(2900-7500)
Cottonwood-Willow Riparian (CW)					
13	3145	23	28	549-1372	(1800-4500)
Juniper Woodland (mixed shrub) (JM)					
9	1080	19	22	793-1342	(2600-4400)
Canotia Mixed Shrub (CA)					
3	265	11	16	884-1189	(2900-3900)
Mesquite Bosque (floodplain woodland) (ME)					
15	3025	18	22	213-915	(700-3000)
Mixed Riparian Scrub (Xeroriparian) (MR)					
16	2640	23	18	229-1220	(750-4000)
Mojave Desertscrub (MD)					
15	1803	25	24	610-1220	(2000-4000)
Sonoran Desertscrub (Arizona Upland) (SD)					
22	3970	33	27	335-1189	(1100-3900)
Creosotebush (Lower Colorado) (CB)					
22	3640	32	18	213-915	(700-3000)

Michigan, Arizona State University, the University of New Mexico, Northern Arizona University, the University of Arizona, the Los Angeles County Museum, and the University of California at Berkeley. In addition, these data were used to compare the past distribution of amphibians and reptiles within the study area with that obtained during the BLM's inventories.

Microhabitat data were collected on each array site and along roads by a modified point-intercept method consisting of 100 sample points separated by 8 m (26 ft) along a randomly determined compass line; on array sites, the center of the line crossed over the array. At each point, the following measurements were taken: (1) vertical distribution of vegetation between 0-0.6 m (0-2 ft), 0.6-1.7 m (2-6 ft), 1.7-6.0 m (6-20 ft), and > 6 m (20 ft) (each time vegetation occurred in a height class above the point, a contact or "hit" was recorded); (2) penetration to the nearest cm into the soil by a pointed metal rod (1 cm in diameter); (3) depth of leaf litter (if present); (4) depth of other litter such as debris heaps (piles of logs, leaves and other dead vegetative material) and rotting logs; (5) characterization of surface rock into size classes of sand, gravel (< 1 cm or 0.4 inches in diameter), cobble (1 to 5 cm or 0.4 to 2 inches in diameter), stone (> 5 cm or 2 inches in diameter), and bed-rock. Vegetation cover and percentage of the surface occupied by each rock and litter size class was determined by comparing the number of "hits" in each category (e.g., litter) with the total number of sample points (100). Plant species were also recorded along each 100 point transect (see table 1 for the number of microhabitat samples taken in each habitat type).

DATA ANALYSIS

I calculated relative abundance of each amphibian and reptile species as

the total number of any species caught during a 24-hour period (array-night). Relative abundance was determined for each species on array sites by taking the greatest number of individuals of a species trapped during a 30-day period and dividing by the number of days. This calculation was used because of monthly differences in species' activity patterns. The number of arrays in which a species was trapped in each habitat type also was compiled to determine how widespread a species was within individual habitat types.

A principal components analysis (Pimental 1979) was performed to compress microhabitat data into a smaller, depictable subset. Mean factor scores of compressed microhabitat data were computed for each habitat type and plotted on a 3 vector (axis) graph. Similarly, mean factor scores of compressed microhabitat data were computed for each amphibian and reptile species (turtles were excluded because aquatic microhabitats were not measured). These scores were calculated for each species by averaging mean factor scores for microhabitats on which a species occurred.

Species richness (total number of species) and species diversity were calculated for each habitat type. Two calculations of species richness for habitats were used; one that used only array data and one that used all data (array, road-riding, and field-search data). In addition, the average number of species collected per array (30-day period) was calculated and compared to overall, array-determined, species richness. Species diversity of each habitat was determined from a Shannon-Weaver diversity index (Hair 1980): $H' = -\sum p_i \log_{10} p_i$; where s = the number of species and p_i is the proportion of the total number of individuals consisting of the i^{th} species. Average species diversity per array was calculated for each habitat type. Because road-riding and field searches did not yield estimates of relative abundance simi-

lar to arrays, only array data were used to calculate species diversity.

Two types of cluster analysis were used to determine similarities among habitat types. The first cluster analysis was performed only on array data, and it was based on euclidean distances (Pimental 1979). Calculation of euclidean distances between habitats were based on a combination of species' presence or absence on a site and similarity in species' dominance (relative abundance) between habitats. Since medium and large snakes (> 0.5 m or 1.5 ft) are not readily caught in pit-fall traps, their relative abundances could not be calculated accurately. To compare the overall herpetofaunas of habitat types, a second cluster analysis was performed. This procedure involved calculation of Simpson similarity coefficients (Pimental 1979). These coefficients were then submitted to a cluster analysis. Unlike the analysis of array data via euclidean distances, the use of Simpson similarity coefficients in a cluster analysis did not consider relative dominance in calculating distances between habitats.

Several thousand site specific distributional records were obtained for amphibians and reptiles within the study (to 16.2 ha or 40 acre accuracy). These individual records were too numerous to report here; detailed locality records for each species are kept at the Bureau of Land Management's Phoenix District Office.

RESULTS

Microhabitats

A principal components analysis (PCA) of microhabitats yielded 3 compressed habitat components (axes), and the cumulative proportion of eigenvalues was < 1.0 with 83% of the variability accounted for by the matrix ($p < .05$). This analysis revealed large differences in the microhabitat among habitat types (fig. 2). Desert grassland, disclimax desert

grassland, and creosotebush habitats had open canopies and low-height vegetative structure, whereas pinyon-juniper, mixed riparian scrub, cottonwood-willow riparian, mixed broadleaf riparian, and ponderosa pine had tree canopies and large amounts of vegetative debris, such as leaf litter and logs, on their surfaces (fig. 2). Closed and open chaparral habitats consisted of shrubs with rocky surfaces, and Sonoran Desert had a combination of trees and shrubs and rocky surfaces (fig. 2).

Species Distributions and Abundances

A total of 28 species of lizards, 30 snakes, 4 turtles, 9 toads, 3 frogs, and 1 salamander were observed or trapped during the study. *Sceloporus*

magister, *Urosaurus ornatus*, *Uta stansburiana*, and *Cnemidophorus tigris* were the most widely distributed and abundant lizards throughout the study area's habitat types (table 2). These lizards also consistently occurred on a large number of sites within each habitat type (table 2). Certain lizards, such as *Gambelia wislizeni*, *Phrynosoma solare*, and *Dipsosaurus dorsalis* occurred only on lower elevation (< 915 m or 3000 ft), desert habitats, and other lizards, such as *Sceloporus undulatus*, *Gerrhonotus kingi*, and *Phrynosoma douglassi* occurred only on higher elevation (> 1220 m or 4000 ft) habitats (table 2). Some species, such as *Eumeces gilberti* and *Cophosaurus texana*, were principally found on higher elevation habitats, but also inhabited cottonwood-willow riparian habitats at lower elevations (549-915 m or 1800-3000 ft) (table 2). Certain lizards, such as

Cnemidophorus burti and *Eumeces obsoletus*, had limited distributions within the study area (table 2); *C. burti* is principally distributed in the Sonoran Desert and Desert Grassland habitats in extreme southern Arizona and Mexico, and *E. obsoletus* only occurs in the chaparral habitat type in the extreme eastern portion of the study area. Although restricted to higher elevation and riparian habitats throughout most of the study area, *C. texana* was found in Sonoran Desert in the extreme eastern portion of the study area. Most lizards occurred throughout the study area where suitable habitat was present and were not restricted by geographic range.

A PCA revealed that lizards differed in their associations with certain microhabitats (fig. 3). Some of the widely distributed species, such as *Cnemidophorus tigris* and *Uta stansburiana*, showed little association with any of the principal components (fig. 3), although the distribution of other common species, such as *Sceloporus magister* and *Urosaurus ornatus* was highly correlated with the presence of vegetation debris (fig. 3). More than half of the lizards occurred on sites with relatively open canopies and shrubs or grasses, and many also preferred rocky substrates (fig. 3). *Dipsosaurus dorsalis*, *Callisaurus draconoides*, and *Gambelia wislizeni* occurred on sites with sand substrate. *Gerrhonotus kingi* and *Eumeces gilberti* occurred on sites with large amounts of vegetative debris, medium to high canopies, and rocky substrates, and *Xantusia vigilis* on sites with similar substrate but with a more open canopy (fig. 3). *Crotaphytus collaris* and *Sauromalus obesus* occurred on sites that were open, rocky, and shrubby or grassy (fig. 3).

Snakes showed similar distributional patterns to lizards. Some snakes, such as *Lampropeltis getulus*, *Pituophis melanoleucus*, *Rhinocheilus lecontei*, *Crotalus atrox*, and *Crotalus molossus*, occurred in many habitat

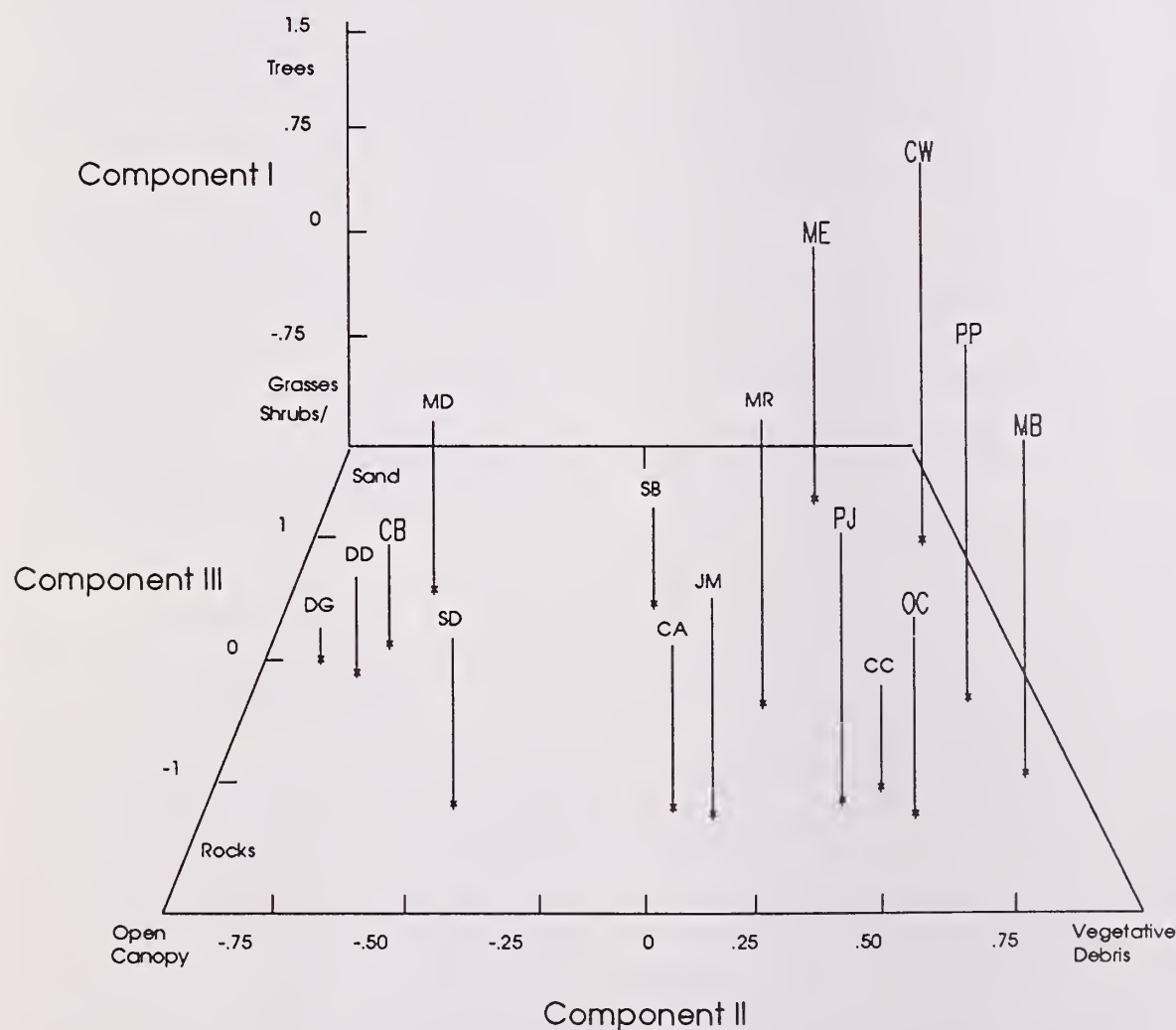


Figure 2.—Mean factor scores of microhabitats for habitat types. (Abbreviations correspond to those listed for habitats in table 1.)

Table 2.—Relative abundance of lizards by habitat type. Relative abundance = the number of an individual species caught in an array per 24 h period. * Indicates species verified in a habitat type via road-riding and searches. The number below the Habitat Type in () = the total number of arrays. The number in () to the right of the species' relative abundance = the number of arrays in which the species was trapped.

PP (5)	PJ (9)	SB (3)	CC (18)	OC (13)	DG (11)	DD (3)	MB (6)	CW (13)	JM (9)	CA (3)	ME (15)	MR (16)	MD (15)	SD (22)	CB (22)
<i>Gerrhonotus kingi</i>															
—	—	—	.03(1)	—	—	—	.03(1)	—	—	—	—	—	—	—	—
<i>Coleonyx variegatus</i>															
.03(1)	—	—	*	.03(1)	.03(1)	—	—	.01(1)	—	.05(2)	.01(5)	.03(8)	.02(6)	.04(11)	.06(11)
<i>Heloderma suspectum</i>															
—	—	—	*	*	—	—	—	.03(1)	*	*	.03(1)	.03(1)	.03(1)	.03(2)	*
<i>Callisaurus draconoides</i>															
—	—	—	.06(1)	—	—	—	—	.10(3)	.01(6)	.05(2)	.03(2)	.05(7)	.08(4)	.06(10)	.04(6)
<i>Cophosaurus texana</i>															
.07(1).09(5)	—	—	.10(5)	.03(1)	—	—	.08(2)	.10(4)	—	—	.01(1)	.03(2)	—	.02(2)	—
<i>Crotaphytus collaris</i>															
—	*	*	.03(2)	*	.10(5)	—	—	*	*	*	—	.03(2)	.03(1)	.04(2)	—
<i>Dipsosaurus dorsalis</i>															
—	—	—	—	—	—	—	—	—	—	—	—	.01(1)	—	.03(1)	.08(9)
<i>Gambelia wislizenii</i>															
—	—	—	—	—	—	.07(1)	—	*	—	—	.01(1)	.03(2)	.01(2)	.02(3)	.02(3)
<i>Holbrookia maculata</i>															
—	—	—	.08(1)	—	.03(1)	—	—	—	—	—	—	—	—	—	—
<i>Phrynosoma douglassi</i>															
.06(3).04(3)	.13(1)	.04(6)	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Phrynosoma platyrhinos</i>															
—	—	—	—	*	—	.07(1)	—	—	.01(1)	.11(3)	—	.03(1)	.02(3)	.02(3)	.05(7)
<i>Phrynosoma solare</i>															
—	—	—	—	—	—	—	—	—	—	—	—	.03(1)	—	.03(2)	.02(1)
<i>Sauromalus obesus</i>															
—	—	—	—	.03(1)	—	—	—	.06(1)	.01(7)	.02(1)	—	.03(1)	*	.02(1)	—
<i>Sceloporus clarki</i>															
—	.03(1)	—	—	—	—	—	.03(2)	.03(2)	—	—	—	.03(1)	.03(1)	.03(1)	—
<i>Sceloporus magister</i>															
—	.05(5)	—	.05(7)	.03(3)	.03(2)	—	.11(4)	.23(7)	.03(8)	.19(3)	.13(10)	.11(16)	.10(15)	.07(14)	.03(6)
<i>Sceloporus undulatus</i>															
.13(3).13(4)	.17(3)	.07(13)	—	.10(3)	—	.02(1)	.04(2)	—	—	—	—	—	—	—	—
<i>Urosaurus graciosus</i>															
—	—	—	—	—	—	—	—	—	—	—	.07(7)	.07(11)	.01(3)	.04(2)	.07(13)
<i>Urosaurus ornatus</i>															
.03(1).04(4)	—	.04(6)	.03(7)	.05(3)	—	.15(4)	.20(5)	.03(1)	—	.08(5)	.04(5)	.03(3)	.06(7)	.02(3)	
<i>Uta stansburiana</i>															
—	.03(2)	—	.04(4)	.04(7)	.05(1)	.10(1)	—	.11(7)	.05(8)	.05(2)	.08(5)	.11(13)	.05(12)	.13(17)	.09(15)
<i>Eumeces gilberti</i>															
.03(1).06(3)	—	.05(9)	.11(10)	.03(1)	—	.02(2)	.04(4)	.03(1)	—	—	—	—	—	—	—
<i>Eumeces obsoletus</i>															
—	—	—	.03(1)	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cnemidophorus burti</i>															
—	—	—	—	—	.09(3)	—	—	—	—	—	—	—	—	—	—
<i>Cnemidophorus flagellicaudus</i>															
—	.05(3)	—	.04(5)	—	.07(2)	—	.08(1)	.02(1)	—	—	—	—	—	—	—
<i>Cnemidophorus inornatus</i>															
—	.03(2)	—	*	—	.03(1)	—	—	—	—	—	—	—	—	—	—

(continued)

Table 2.—(continued).

PP (5)	PJ (9)	SB (3)	CC (18)	OC (13)	DG (11)	DD (3)	MB (6)	CW (13)	JM (9)	CA (3)	ME (15)	MR (16)	MD (15)	SD (22)	CB (22)
<i>Cnemidophorus tigris</i>															
.02(1)	.12(6)	—	.07(6)	.05(3)	.09(4)	.23(2)	.10(3)	.07(7)	.14(9)	.25(3)	.14(9)	.25(16)	.13(15)	.17(21)	.15(21)
<i>Cnemidophorus uniparens</i>															
—	—	—	.04(1)	—	.03(1)	—	—	—	—	—	—	—	—	—	—
<i>Cnemidophorus velox</i>															
—	*	.49(3)	.14(5)	—	.01(1)	—	.05(2)	.02(2)	—	—	—	—	—	—	—
<i>Xantusia vigilis</i>															
—	.02(1)	—	.05(1)	.08(7)	—	—	—	—	.01(1)	—	—	—	.07(1)	*	—
Total Number of Species (includes species verified by road-riding and searches)															
7	14	4	20	12	14	4	10	16	11	9	10	16	14	17	12
Mean Relative Abundance															
.37	.69	.79	.96	.43	.74	.47	.67	1.06	.54	.72	.59	.91	.58	.78	.63
Species Diversity (H')															
.56	1.00	.40	1.18	.89	1.07	.54	.91	1.00	.76	.72	.86	1.05	1.00	1.09	.95

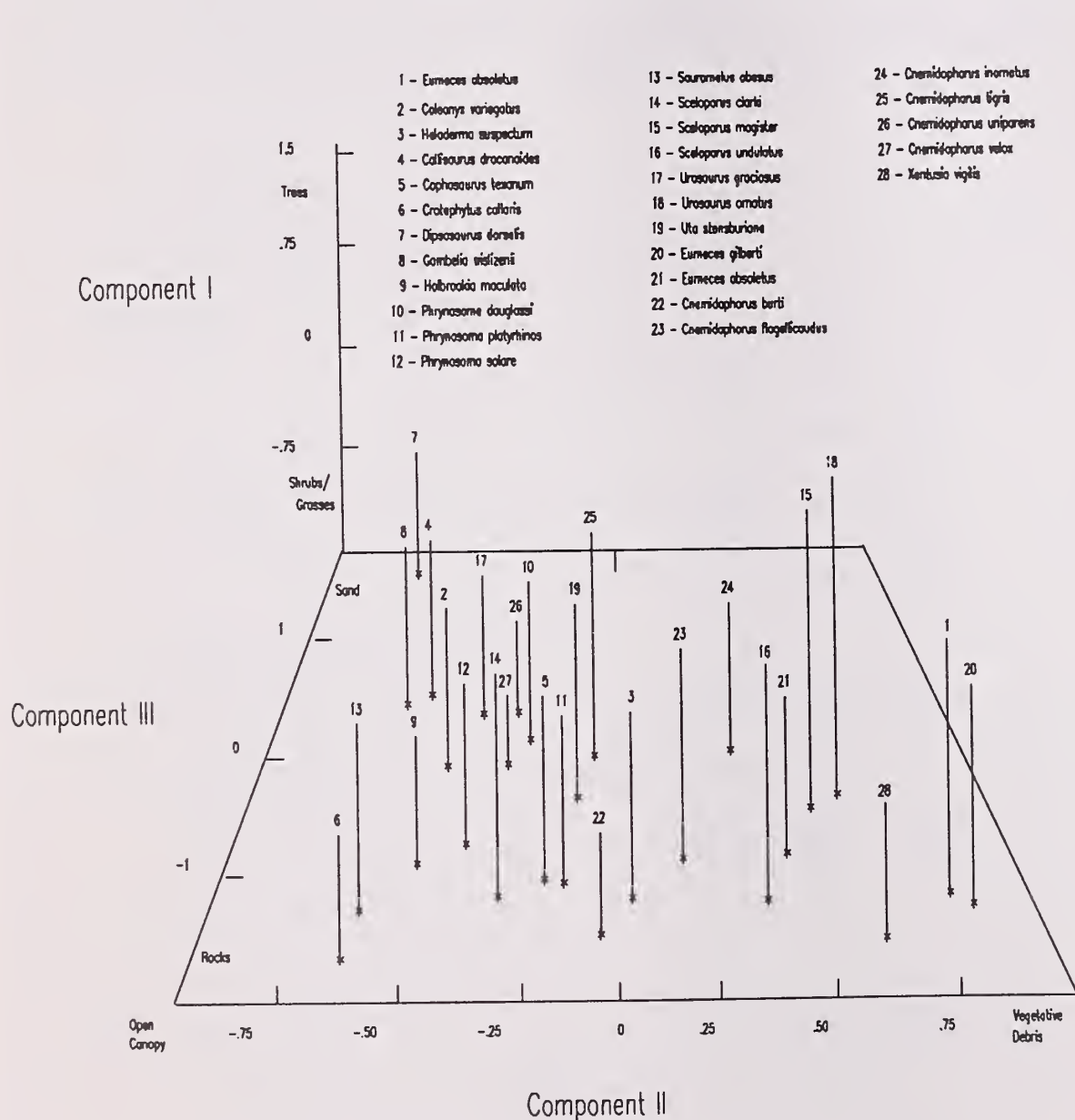


Figure 3.—Mean factor scores of microhabitats for lizards.

types. Others, such as *Chilomeniscus cinctus*, *Chionactis occipitalis*, *Phyllorhynchus browni*, *Phyllorhynchus decurtatus*, and *Crotalus cerastes*, occurred primarily on lower elevation (< 915 m or 3000 ft), desert habitats, and some, such as *Lampropeltis pyromelana* and *Crotalus viridis cerberus*, occurred only on higher elevation (>1525 m or 5000 ft) habitats (table 3). *Lichanura trivirgata* and *P. browni* occur primarily outside the study areas, and their distributions only overlap the extreme southern and southwestern portions of the study area. Therefore, they were limited to the small number of sites with suitable habitat. *Thamnophis cyrtopsis* and *Thamnophis marcianus* were restricted to sites with water, with the former occurring on a large number of habitats and the latter only in a mesquite bosque habitat along the Gila River south of Phoenix. Similar to *Cophosaurus texana*, *Tantilla hobartsmithii* was found on higher elevation (>1220 m or 4000 ft) and riparian habitats throughout most of the study area, but also in Sonoran Desert in the eastern portion of the study area.

A PCA of microhabitats on which snakes occurred revealed that, simi-

Table 3.—Relative abundance of snakes by habitat type. Relative abundance = the number of an individual species caught in an array per 24 h period. * indicates species verified in a habitat type via road-riding and searches. The number below the Habitat Type in () = the total number of arrays. The number in () to the right of the species' relative abundance = the number of arrays in which the species was trapped.

PP (5)	PJ (9)	SB (3)	CC (18)	OC (13)	DG (11)	DD (3)	MB (6)	CW (13)	JM (9)	CA (3)	ME (15)	MR (16)	MD (15)	SD (22)	CB (22)
<i>Arizona elegans</i>	—	*	—	*	—	—	—	—	*	*	—	*	.02(1)	*	.03(2)
<i>Chilomeniscus cinctus</i>	—	—	—	—	—	—	—	.05(3)	—	—	.07(7)	.08(7)	—	.02(2)	.03(1)
<i>Chionactis occipitalis</i>	—	—	—	—	—	—	—	—	—	—	.03(3)	.12(2)	—	.05(4)	.06(5)
<i>Diadophis punctatus</i>	—	*	—	*	.02(2)	*	—	*	*	—	—	—	—	.02(1)	—
<i>Hypsiglena torquata</i>	—	—	—	*	—	—	.03(2)	*	.03(2)	.02(1)	.02(1)	*	.02(1)	*	—
<i>Lampropeltis getulus</i>	—	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Lampropeltis pyromelana</i>	*	—	—	—	—	—	*	—	—	—	—	—	—	—	—
<i>Lichanura trivirgata</i>	—	—	—	*	—	—	—	*	*	—	—	—	—	*	—
<i>Masticophis bilineatus</i>	—	—	—	.03(2)	.03(1)	—	*	*	*	—	—	—	—	—	—
<i>Masticophis flagellum</i>	—	.03(1)	—	*	—	—	—	.02(1)	*	.02(1)	.02(1)	.02(1)	.02(1)	.02(1)	.03(2)
<i>Masticophis taeniatus</i>	*	*	*	*	.03(2)	.03(2)	—	.02(1)	*	—	—	—	—	—	—
<i>Pituophis melanoleucus</i>	—	*	*	*	*	—	.02(1)	*	.02(1)	*	.02(1)	*	*	*	.01(1)
<i>Phyllorhynchus browni</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	*	*
<i>Phyllorhynchus decurtatus</i>	—	—	—	—	—	—	—	—	—	—	—	.02(2)	—	*	.03(2)
<i>Rhinocheilus leonti</i>	—	*	—	*	*	—	.02(1)	.02(1)	*	*	*	*	*	.02(1)	.02(1)
<i>Salvadora hexalepis</i>	—	—	—	.02(1)	.02(1)	*	—	.03(2)	*	.03(1)	.03(1)	.02(1)	.04(2)	.02(1)	*
<i>Sonora semiannulata</i>	—	—	—	*	*	.10(2)	—	—	*	.03(1)	*	*	—	*	.05(3)
<i>Tantilla hobartsmithii</i>	—	—	—	.05(5)	.08(8)	.07(2)	—	.02(1)	.05(4)	.03(1)	—	.03(2)	—	*	—
<i>Thamnophis cyrtopsis</i>	*	*	*	*	—	—	*	*	*	*	*	*	*	*	—
<i>Thamnophis marcianus</i>	—	—	—	—	—	—	—	—	—	—	*	—	—	—	—
<i>Trimorphodon biscutatus lambda</i>	—	—	—	*	—	—	—	.02(1)	*	*	—	*	*	*	*
<i>Crotalus atrox</i>	—	*	—	*	*	—	*	*	*	*	*	*	*	*	*
<i>Crotalus cerastes</i>	—	—	—	—	—	—	—	—	—	—	*	*	*	*	.02(2)
<i>Crotalus mitchelli</i>	—	—	—	*	*	*	—	—	*	*	*	*	*	*	—

(continued)

Table 3.—(continued).

PP (5)	PJ (9)	SB (3)	CC (18)	OC (13)	DG (11)	DD (3)	MB (6)	CW (13)	JM (9)	CA (3)	ME (15)	MR (16)	MD (15)	SD (22)	CB (22)
<i>Crotalus molossus</i>	—	*	*	*	*	—	*	*	*	*	—	*	*	*	—
<i>Crotalus scutulatus</i>	—	—	—	—	—	—	—	—	—	—	.02(1)	*	*	*	*
<i>Crotalus tigris</i>	—	—	—	*	—	—	—	—	—	—	—	—	—	*	—
<i>Crotalus viridis cerberus</i>	*	*	*	*	*	—	*	—	—	—	—	—	—	—	—
<i>Micruroides euryxanthus</i>	—	—	—	*	—	—	—	*	—	—	.03(2)	—	—	*	—
<i>Leptotyphlops humilis</i>	—	.04(3)	—	—	*	—	—	.05(2)	.05(3)	.05(3)	—	.09(6)	.03(2)	.02(1)	.03(2)
Total Number of Species (includes species verified by road-riding and searches)															
4	11	6	17	22	12	2	12	20	18	13	17	18	16	25	16
Mean Relative Abundance															
—	.07	—	.07	.18	.23	—	.18	.24	.16	.07	.36	.28	.12	.22	.29
Species Diversity (H')															
—	.30	—	.26	.63	.54	—	.75	.81	.68	.47	.93	.68	.68	.86	.90

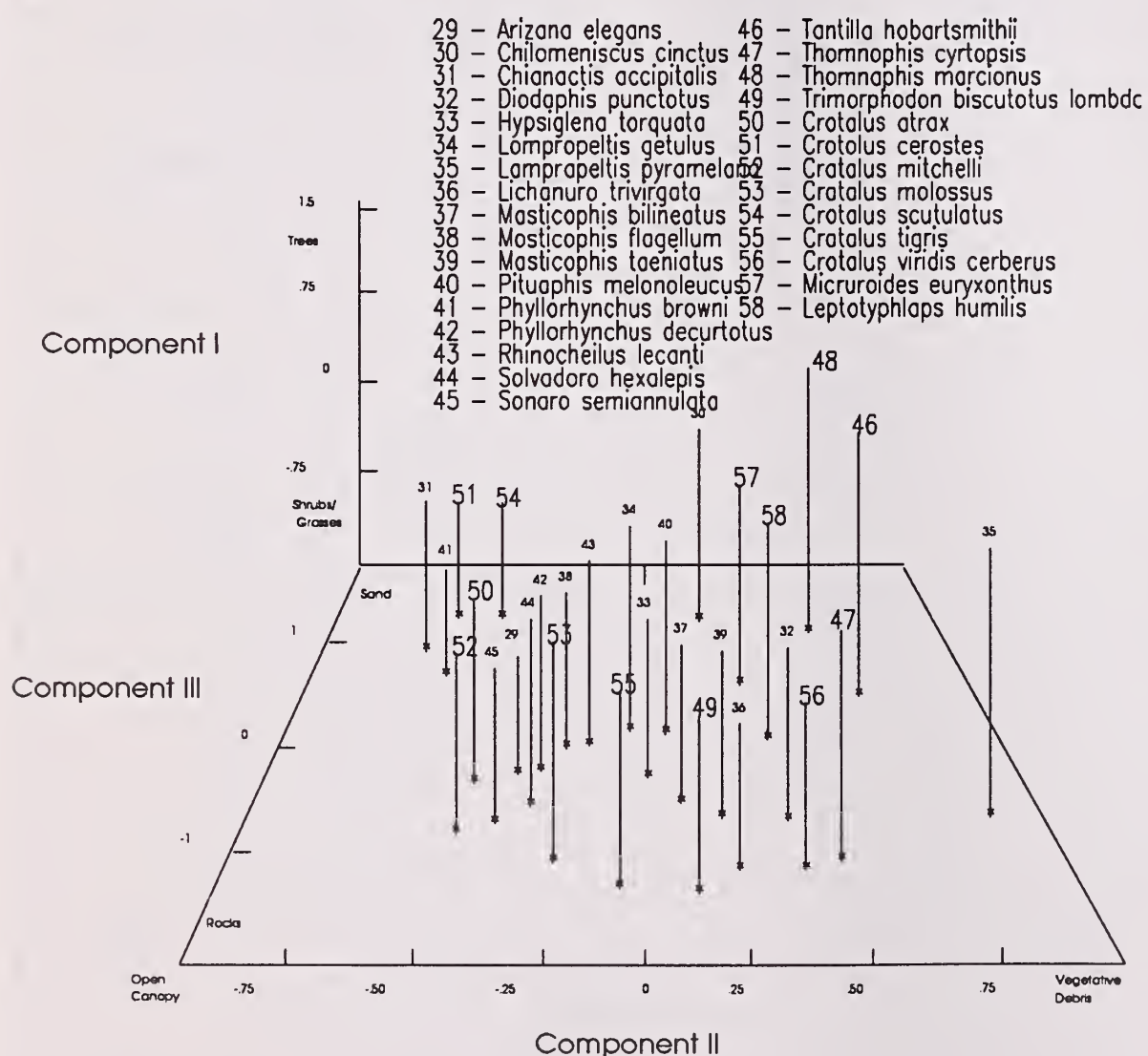


Figure 4.—Mean factor scores of microhabitats for snakes.

lar to those of lizards, microhabitat associations differed among snakes (fig. 4). Many of the widely distributed snakes, such as *Hypsiglena torquata*, *Lampropeltis getulus*, *Masticophis flagellum*, and *Pituophis melanoleucus*, showed no strong relationship with any of the compressed habitat components (fig. 4). Conversely, most species with limited distributions showed a strong relationship with certain components (fig. 4). *Chionactis occipitalis*, *Crotalus cerastes*, *Crotalus scutulatus*, and *Phyllorhynchus browni* consistently occurred on open, sandy sites, and *Chilomeniscus cinctus* occurred on sites with sandy substrate but taller canopy (fig. 4). Other species, such as *Crotalus mitchelli* and *Sonora semiannulata*, were found on sites with open canopies but rocky substrates (fig. 4). *Thamnophis marci* and *Tantilla hobartsmithii* occurred on sites with sandy substrates but closed canopies and large amounts of vegetative debris, and *Lampropeltis pyromelana* occurred only on sites with high amounts of vegetative debris (fig. 4). Other species, such as *Diadophis*

punctatus, *Thamnophis cyrtopsis*, and *Crotalus viridis cerberus*, occurred on rocky sites with high amounts of vegetative debris (fig. 4).

Except for a single *Gopherus agassizii* captured in an array, all turtle records came from road-riding and field searches. Four species of turtles were recorded within the study area, three aquatic and one terrestrial (table 4). Of these, *G. agassizii* was the most widely distributed (verified in 9 habitat types, table 4). A more thorough account of this turtle's distribution is described by Burge (1979, 1980). *Pseudemys scripta*, an introduced species, was limited to a stretch of the Gila River from the 99th Street bridge in southwest Phoenix to Gillespie Dam, located approximately 24 km (15 miles) south of Buckeye. *Trionyx spiniferus* occurred at Alamo Lake (confluence of the Big Sandy and Santa Maria rivers in western Arizona) and along perennial stretches of the Gila River from Phoenix to Yuma. *Kinosternon sonoriense* occurred on several permanent streams and rivers throughout the study area.

In contrast to the observed distribution patterns among lizards and snakes, the distribution of amphibians did not show an elevational pattern. Although certain species such

as *Bufo punctatus* and *Scaphiopus couchi* occurred in a large number of habitat types, most species were found in at least one lower (< 915 m or 3000 ft) and one higher (> 1220 m or 4000 ft) elevation site (table 5). Similar to lizards and snakes, there are some amphibians whose ranges are principally outside the study area and are, therefore, found only on a few sites (table 5). The ranges of *Bufo debilis*, *Bufo retiformes*, and *Gastrophyrne olivacea* are primarily in northern Mexico, or east and south of the study area in the Chihuahuan Desert; within the study areas, their ranges are limited to desert grassland habitats in the extreme southern portion (Vekol Valley, 48 km or 30 mi west-southwest of Casa Grande). All populations of *Ambystoma tigrinum* were located at earthen stock tanks (dirt tanks). Presumably, all of these populations were introduced.

A PCA demonstrated correlations between occurrence of amphibian species and particular microhabitats (fig. 5). *Bufo debilis*, *B. retiformes*, and *Gastrophyrne olivacea* occurred on sandy, grassy sites, and *Bufo cognatus* on sandy, shrubby sites (fig. 5). *Bufo microscaphus* and *B. punctatus* occurred on rocky sites, and *Hyla arenicolor* on rocky sites generally occupied by trees and large amounts of

vegetation debris (fig. 5). Certain species, such as *Scaphiopus couchi*, *Bufo alvarius*, and *Bufo woodhousei* occurred on sites with a wide variety of substrates (fig. 5).

The occurrence and frequency of water was not quantitatively measured at each site; therefore, the influence of water was not considered in the development of figure 5. However, all sites with amphibians had surface water during some part of the year, especially during summer months. All sites with *Bufo microscaphus*, *Rana pipiens*, *R. catesbeiana*, and *Hyla arenicolor* had permanent water (e.g., springs, creeks, and rivers).

At the start of the survey in 1977, populations of *Bufo microscaphus* and *B. woodhousei* sympatric on major drainages, such as the Hassayampa, Santa Maria, Agua Fria, and New rivers, could be easily distinguished from one another. By 1981, populations on all of these drainages were indistinguishable.

Range Extensions

Thirty-five range extensions were recorded for amphibians and reptiles within the study area. Except for the following discussion, range exten-

Table 4.—Distribution of turtles by habitat type (*). Records are entirely from road-riding and searches (except where otherwise indicated. All turtles except *Gopherus agassizii* occurred only at sites with permanent water within habitat types listed below.

PP	PJ	SB	CC	OC	DG	DD	MB	CW	JM	CA	ME	MR	MD	SD	CB
<i>Gopherus agassizii</i>															
—	—	—	*	*	—	—	—	*	*	*	**	*	*	*	—
<i>Pseudemys scripta</i>															
—	—	—	—	—	—	—	—	—	—	—	*	—	—	—	—
<i>Trionyx spiniferus</i>															
—	—	—	—	—	—	—	—	—	—	—	*	—	—	—	—
<i>Kinosternon sonoriense</i>															
—	—	—	—	—	—	—	*	*	—	—	*	—	—	—	—
** Trapped in an array															
Number of species															
—	—	—	1	1	—	—	1	2	1	1	4	1	1	1	—

Table 5.—Relative abundance of amphibians by habitat type. Relative abundance = the number of an individual species caught in an array per 24 h period. * Indicates species verified in a habitat type via road-riding and searches. The number below the Habitat Type in () = the total number of arrays. The number in () to the right of the species' relative abundance = the number of arrays in which the species was trapped.

PP (5)	PJ (9)	SB (3)	CC (18)	OC (13)	DG (11)	DD (3)	MB (6)	CW (13)	JM (9)	CA (3)	ME (15)	MR (16)	MD (15)	SD (22)	CB (22)
<i>Bufo alvarius</i>	—	—	.07(1)	*	.06(2)	—	—	.03(2)	—	—	.03(4)	*	*	*	—
<i>Bufo cognatus</i>	—	*	—	—	.14(3)	*	—	—	—	—	.09(3)	—	—	—	.06(4)
<i>Bufo debilis</i>	—	—	—	—	.03(1)	—	—	—	—	—	*	—	—	—	—
<i>Bufo microscaphus</i> ¹	*	*	.05(2)	—	*	—	.13(3)	.06(3)	*	—	.07(4)	—	—	—	—
<i>Bufo punctatus</i>	.03(1).03(1)	*	.15(8)	.11(8)	—	—	.20(1)	.16(3)	.12(2)	.23(1)	.28(6)	.05(2)	.06(2)	.10(7)	—
<i>Bufo retiformis</i>	—	—	—	—	.18(2)	—	—	—	—	—	—	—	—	—	—
<i>Bufo woodhousei</i> ¹	—	—	—	—	—	—	—	*	—	—	—	.03(1)	—	*	*
<i>Hyla arenicolor</i>	*	*	.07(1)	.03(1)	—	—	*	—	*	*	—	*	*	*	—
<i>Gastrophyrne olivacea</i>	—	—	—	—	.05(2)	—	—	—	—	—	—	—	—	—	—
<i>Scaphiopus couchi</i>	—	—	*	.12(2)	.10(3)	*	—	*	*	*	.15(6)	.06(2)	.07(6)	.06(5)	.11(6)
<i>Rana pipiens</i>	*	*	*	*	—	—	*	.20(1)	*	*	*	*	*	*	—
<i>Rana catesbeiana</i>	—	—	—	—	—	—	—	—	—	—	.03(1)	—	—	—	—
<i>Ambystoma tigrinum</i>	—	—	—	*	*	—	—	—	—	*	—	—	—	—	—

¹95% of these were a cross between the two species (*B. microscaphus* x *B. woodhousei*)

Total Number of Species (includes species verified by road-riding and searches)

Total Number of Species (M)	4	4	3	6	6	8	2	4	6	5	5	8	6	5	6	3
Mean Relative Abundance	.03	.03	—	.34	.26	.56	—	.33	.45	.12	.23	.65	.14	.13	.16	.17
Species Diversity (H')	—	—	—	.56	.42	.71	—	.29	.51	—	—	.65	.46	.30	.29	.28

sions discovered during this study have been described elsewhere (Jones et al. 1981, Jones et al. 1982, Buse 1983, Jones et al. 1983, Jones et al. 1985). The southernmost distribution of *Tantilla hobartsmithii* was extended from the Salt River east of Phoenix, southwest in the mesquite bosque habitat along the Gila River to 56 km (35 miles) east-northeast of Yuma (fig. 6). A population of *T. hobartsmithii* was also discovered in a 10 ha

(25 acres) open chaparral habitat in the Eagletail Mountains (fig. 6). The westernmost distribution of *Cnemidophorus burti* was extended from the Tucson area northwest by discovery of isolated populations in desert grassland habitats on summits of the Tabletop and Estrella mountains (fig. 6).

An isolated population of *Masticophis bilineatus lineolatus* was discovered on the summit of Tabletop

Mountain in a relict desert grassland habitat (fig. 6). This population extends the known distribution of this subspecies approximately 100 km (62 mi) to the north of the only other known population (Ajo Mountains).

Finally, an isolated population of *Diadophis punctatus* was discovered in a relict desert grassland community on the summit of the Estrella Mountains southwest of Phoenix (fig. 6).

Comparison of Habitat Types

Based on data compiled from pit-fall trapping, road-riding, and searches, the Sonoran Desert habitat had the greatest species richness (49 species, fig. 7). Closed chaparral and cottonwood-willow riparian habitats were the second richest habitats (44 species), and open chaparral and mixed riparian scrub were third (41 species, fig. 7).

Disclimax desert grassland had the fewest species (8), and sagebrush and ponderosa pine had the second and third fewest species (13 and 15 species, respectively, fig. 7). All other habitats had at least 27 species but not more than 39 (fig. 7). Although Sonoran Desert had the richest lizard and snake faunas, mesquite bosque and desert grassland habitats had the richest amphibian fauna (fig. 7). The mesquite bosque habitat type had the

greatest number of turtle species (four species, fig. 7).

When only array data are compiled, disclimax desert grassland, sagebrush, and ponderosa pine habitats still had by far the lowest number of species, but Sonoran Desert and mesquite bosque had the greatest number of species (fig. 8). As when all data were taken into account, mixed riparian scrub, cottonwood-willow riparian, closed chaparral, and open chaparral had high species richness (fig. 8). However, desert grassland was relatively more diverse using only array data (fig. 8).

The difference between array vs. all data appears to result from the inability of arrays to consistently verify (trap) turtles and medium and large snakes, although many larger snake species were verified because young-of-the-year were easily trapped.

A more revealing statistic is the average number of species verified by an array (fig. 8). This analysis reveals which habitats consistently had the largest number of species at sample sites. Certain habitats, such as desert grassland, although high in overall species richness, had relatively few species verified at each array site (fig. 8). Other habitats, such as ponderosa pine, sagebrush, and disclimax desert grassland, had the lowest number of total species and the lowest average number of species per array site (fig. 8). Many of the habitats that had high overall species richness also had high overall richness at each array site; however, cottonwood-willow had a higher average number of species per array site than did Sonoran Desert (fig. 8).

Species diversity indices (H') calculated from array data reveal patterns similar to those described above (fig. 9). Disclimax desert grassland, sagebrush, and ponderosa pine continue to exhibit low diversity, and Sonoran Desert, closed chaparral, cottonwood-willow riparian, mixed riparian scrub, and desert grassland continue to be diverse (fig. 9). However, as in the previous analysis, the average diversity per array site is low when compared to total diversity for individual habitats (fig. 9). Of the habitats with high overall diversity, mixed broadleaf riparian and cottonwood-willow riparian had relatively high average diversity per array site (fig. 9).

A comparison of herpetofaunas of each habitat type by cluster analyses revealed that all desert habitats, such as creosotebush, Sonoran Desert, Mohave Desert, and mixed riparian scrub had very similar herpetofaunas (figs. 10 and 11). In both cluster analyses, open and closed chaparral had similar herpetofaunas, and sagebrush and disclimax desert grassland had a herpetofauna different from any other habitat. However, there were differences in results of the two cluster analyses for other habitats. Whereas the cluster analysis of array

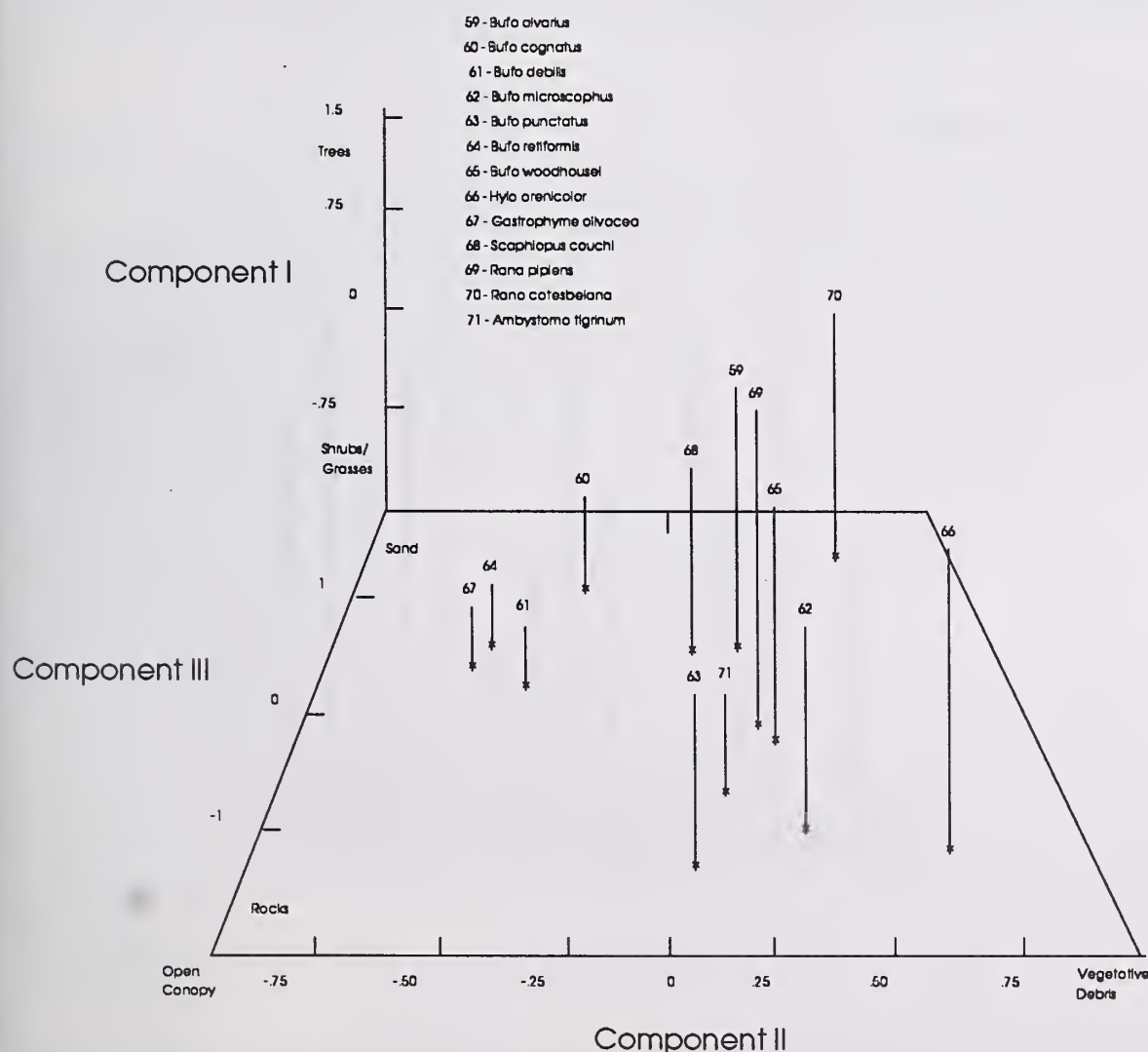


Figure 5.—Mean factor scores of microhabitats for amphibians.

data revealed large differences between the herpetofaunas of cottonwood-willow and desert habitats, such as Sonoran and Mohave Deserts, these habitats had a relatively moderate degree of overlap when all data were analyzed (figs. 10 and 11). Additionally, ponderosa pine and pinyon-juniper habitats were similar when array data were analyzed and relatively dissimilar when all data were submitted to cluster analysis (figs. 10 and 11).

DISCUSSION

Overall, western Arizona has an extremely diverse herpetofauna, primarily because of its large variety of habitats zoogeographic location. The Hualapai Mountains, located in northwestern Arizona, are adjacent to three major deserts: the Mohave Desert to the northwest, the Great Basin Desert to the northeast, and the Sonoran Desert to the south. Nowhere else on the North American continent does such a phenomenon exist. The diversity of habitat in this area is also enhanced by the occurrence of several woodland islands.

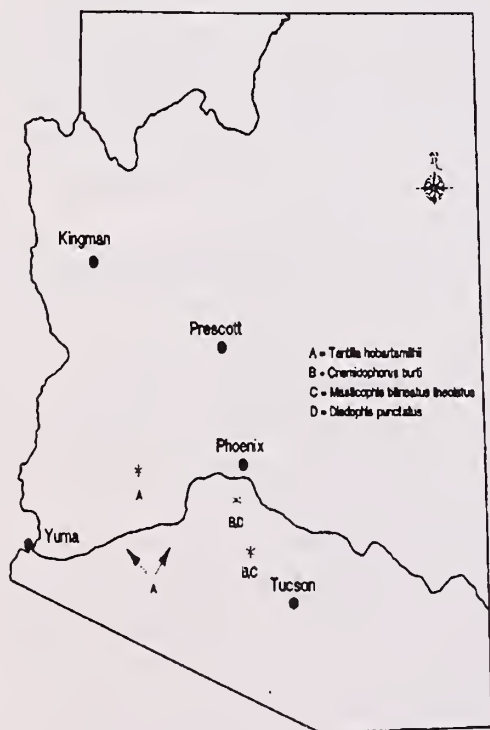


Figure 6.—Map of range extensions.

Number of Species

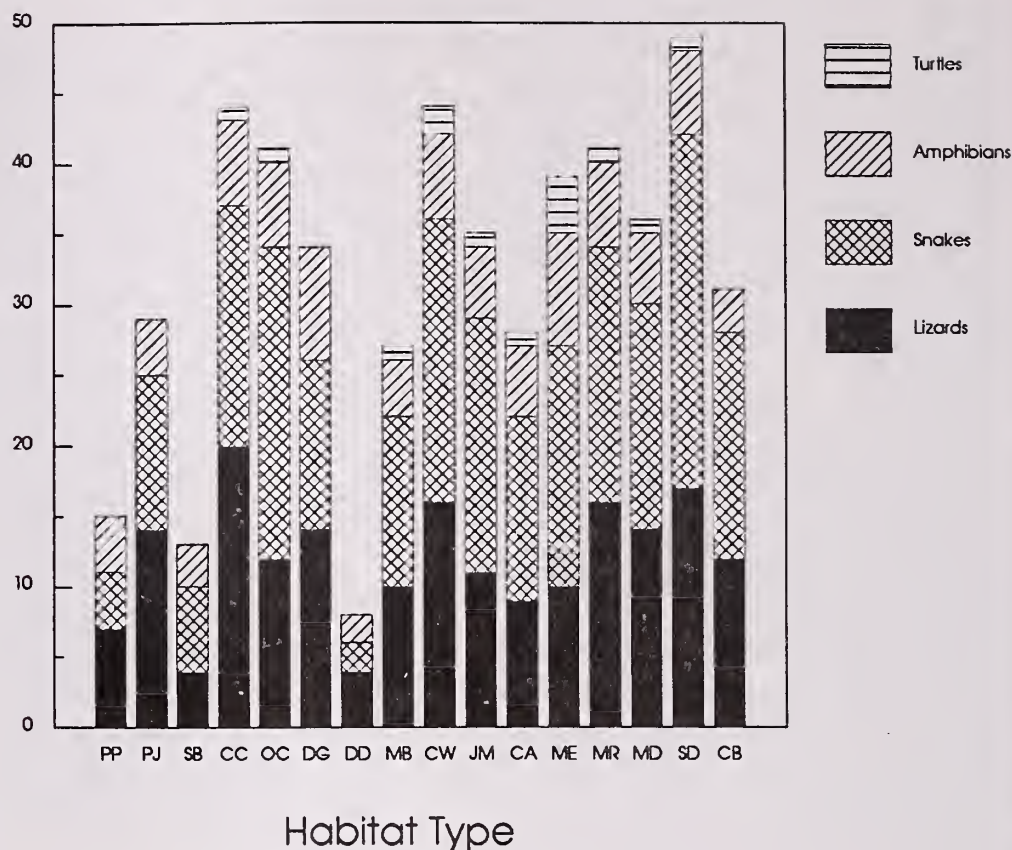


Figure 7.—Number of species by taxonomic group by habitat type. (Abbrev. correspond to those listed for habitats in table 1.)

Number of Species

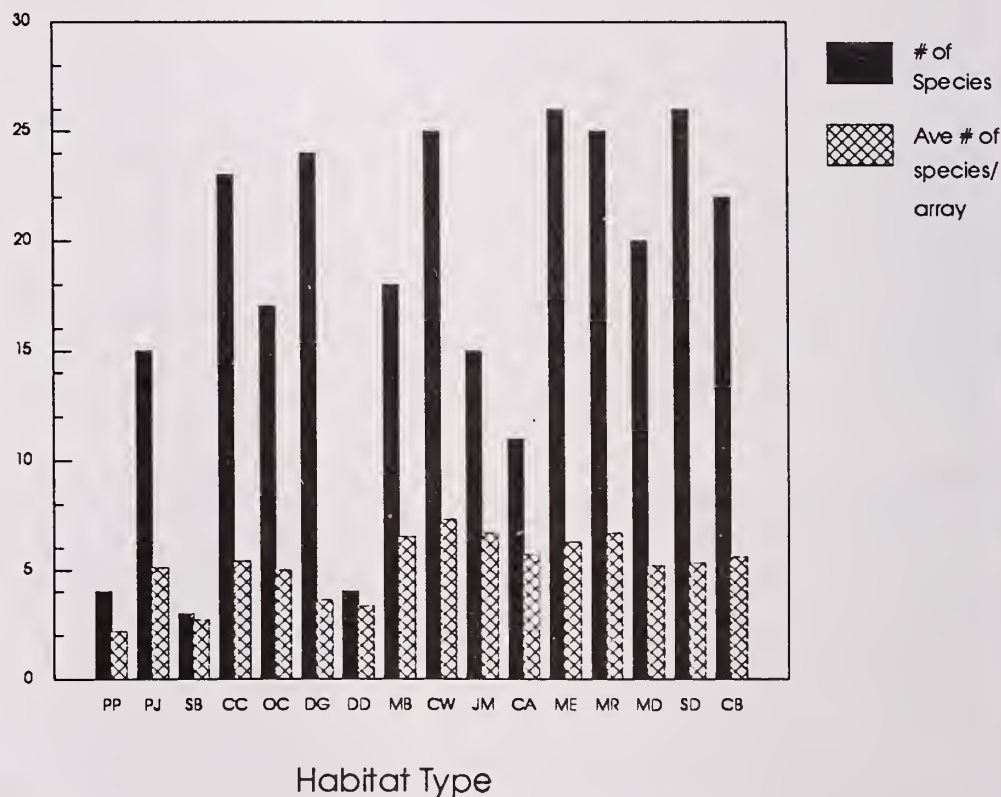


Figure 8.—Total number of species caught in arrays by habitat type vs. the average number of species caught per array by habitat type. (Abbrev. correspond to those listed for habitats in table 1.)

Species Diversity (H')

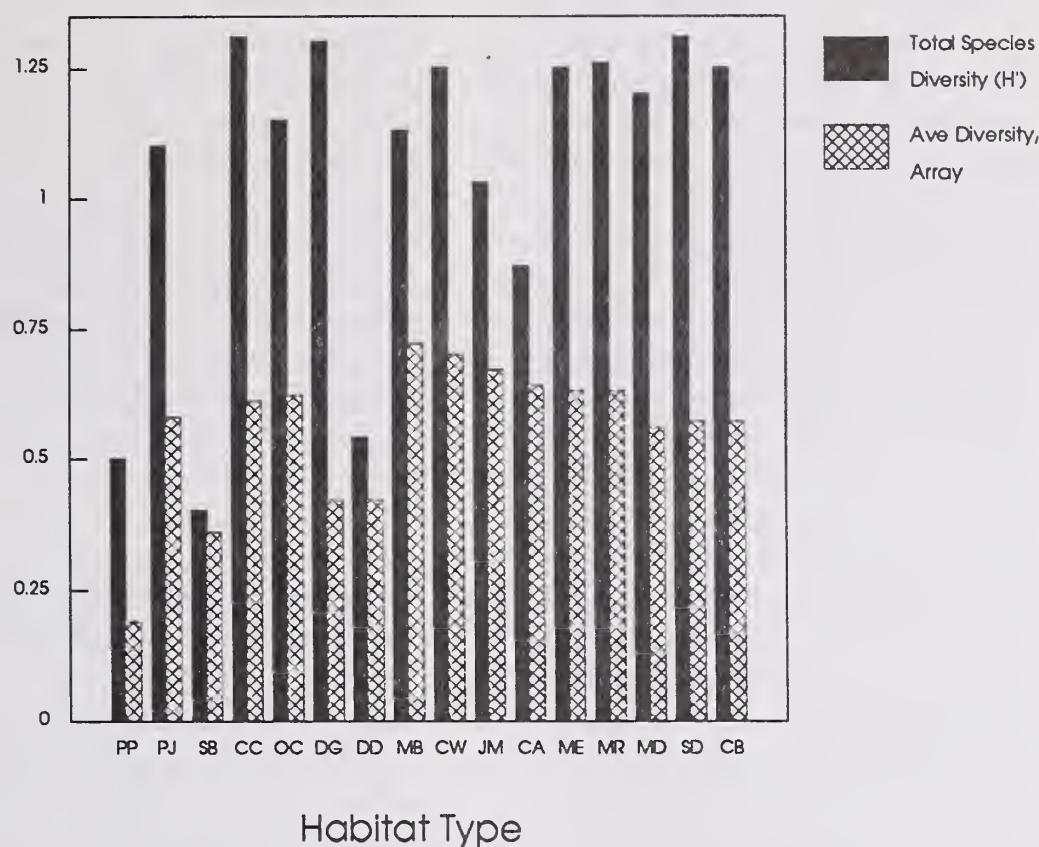


Figure 9.—Total species diversity (H') by habitat type vs. average species per array by habitat type. (Abbrev. correspond to those listed for habitats in table 1.)

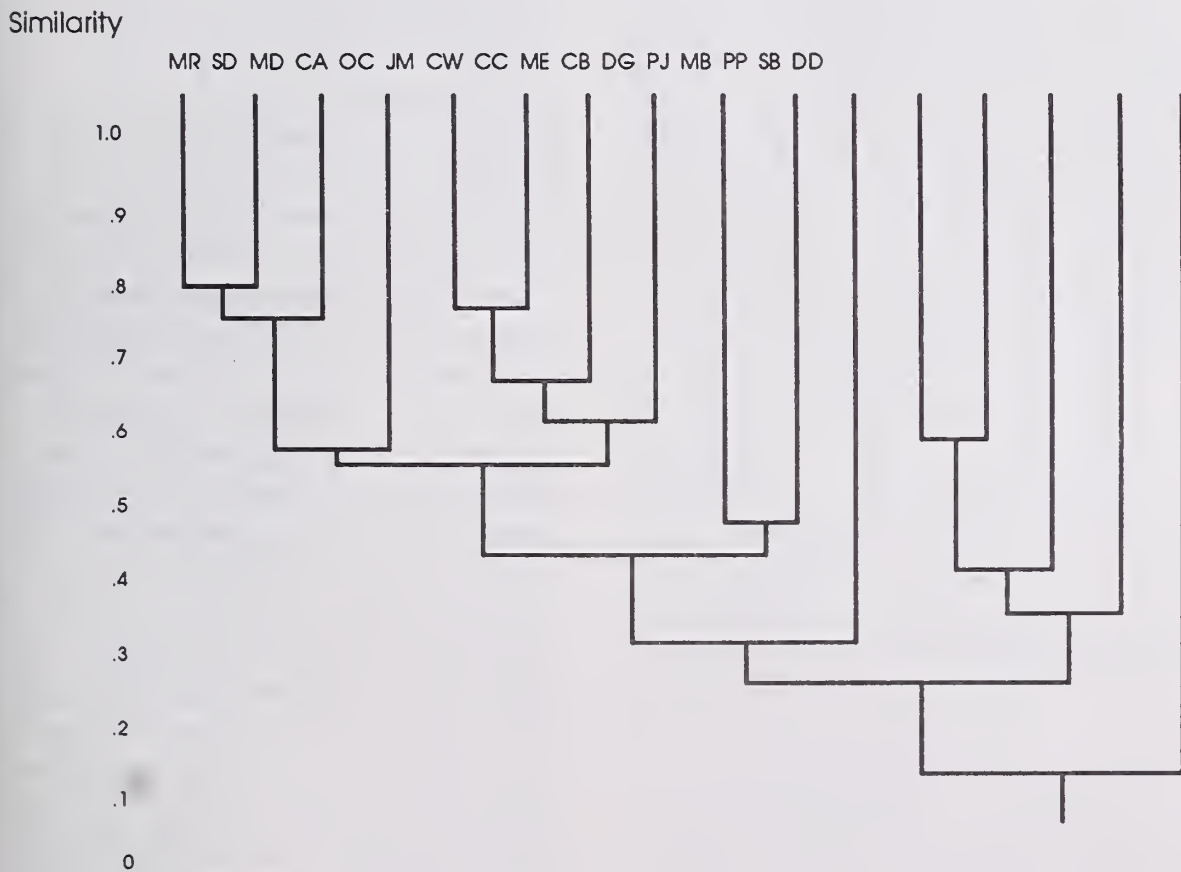


Figure 10.—Cluster analysis (dendrogram) of array data illustrating similarities in habitat type herpetofaunas. (Abbrev. correspond to those listed for habitats in table 1.)

Patterns of Species Distributions

This survey reveals that certain species are widespread, occurring in several habitats, but many species are limited to specific habitat types. Also, some species occur on most sample sites within a habitat type and others on only a few. There appear to be at least 3 major factors contributing to distributional patterns of amphibians and reptiles in the study area.

Geographic Limitations

The ranges of certain species only peripherally occur in western Arizona. *Cnemidophorus burti*, *Phyllorhynchus browni*, *Masticophis bilineatus lineolatus*, and *Bufo retiformis* occur principally in northern Mexico whereas others such as *Holbrookia maculata*, *Eumeces obsoletus*, *Gastrophyrne olivacea*, and *Bufo debilis* are mostly east and north of the study area (Stebbins 1985). *Bufo retiformis*, *Gastrophyrne olivacea*, and *Bufo debilis* are associated with low elevation (457-915 m or 1500-3000 ft) desert grassland (Jones et al. 1983), and these habitats are mostly absent in the central and northern portions of the study area. However, habitat suitable for other species listed above appears to be available throughout most of the study area.

Physical barriers, such as topography, elevation, and climate may have presented these species from colonizing or immigrating into suitable habitats to the north and west (see Connor and Simberloff 1979, Case 1983, Jones et al. 1985 for discussion of the influence of physical barriers on colonization/immigration). In addition, competition between species may have limited individual species' ranges during initial and subsequent colonization of suitable habitats (e.g., during periods of large climatic changes). Perhaps the best example of this is the distributional relationship between *Eumeces gilberti* and *E.*

obsoletus. *E. gilberti* belongs to the skiltonianus group of skinks, whose evolutionary center is the western United States (Taylor 1935, Rogers and Fitch 1947).

Conversely, *E. obsoletus* evolved in the Great Plains region (Fitch 1955). Both of these lizards occupy seemingly identical, but separate, habitats in central Arizona, and their distributions come together in chaparral and desert grassland habitat types near Cordes Junction; the westernmost range of *E. obsoletus* is just east of Interstate Highway 17 and the easternmost range of *E. gilberti* is just west of the highway. These lizards are similar in appearance, with *E. obsoletus* averaging slightly larger in size.

Although subtle differences in microhabitat cannot be ruled out as factors influencing their ranges, it ap-

pears that these lizards are mutual exclusive (competitive exclusion).

Several remnant stands of chaparral and desert grassland occur in western and northwestern Arizona at or near the summits of mountain ranges. These relict stands or habitat islands are isolated within creosotebush and Sonoran Desert habitats as a result of the retreat of the last Ice Age (see Van Devender and Spaulding 1977). Data collected in my study show that several reptiles typically found in "upland" habitats (e.g., large continuous stands of desert grassland and woodlands associated with the Colorado Plateau of central and northern Arizona) inhabit these isolated mountain stands, although the number and composition of these upland species vary among mountains. Habitat island size appears to be of primary importance in

determining the number of upland present species (see Jones et al. 1985).

The turtles *Pseudemys scripta* and *Trionyx spiniferus* are present along the Gila River as a result of introductions. *P. scripta* is a popular pet, and specimens have been released along the Gila River in southwest Phoenix. *T. spiniferus* was introduced along the Colorado River in the early 1900's (Stebbins 1985); presumably, these populations expanded into the Gila River at the confluence of the Gila and Colorado rivers near Yuma.

Microhabitats and Physical Characteristics of Habitat

Many studies have shown a strong relationship between the distribution and abundance of amphibians and reptiles and the presence and amount of certain microhabitats (Norris 1953, Pianka 1966, Zweifel and Lowe 1966, Fleharty 1967, Pianka and Parker 1972). The distribution of a number of species within western Arizona area appears to be influenced by the presence of microhabitats on sites, although most of the widespread species, such as *Cnemidophorus tigris*, *Pituophis melanoleucus*, and *Lampropeltis getulus* show no strong relationship with any specific habitat components, others (e.g., *Urosaurus ornatus* and *Sceloporus magister*) occur on sites with trees and downed litter. Many sites in the study area, including desert and upland habitat types, have trees and downed logs, and this probably accounts for these species' wide distributions. The habitat analysis revealed that several species are associated with specific substrate types (e.g., rock), density or height of the vegetation canopy, type of vegetation (shrubs or grasses vs. trees), or presence of downed litter.

Species' associations with certain microhabitats may reflect their physical or behavioral limitations. For example, *Eumeces gilberti* may be restricted to sites with large amounts

Similarity

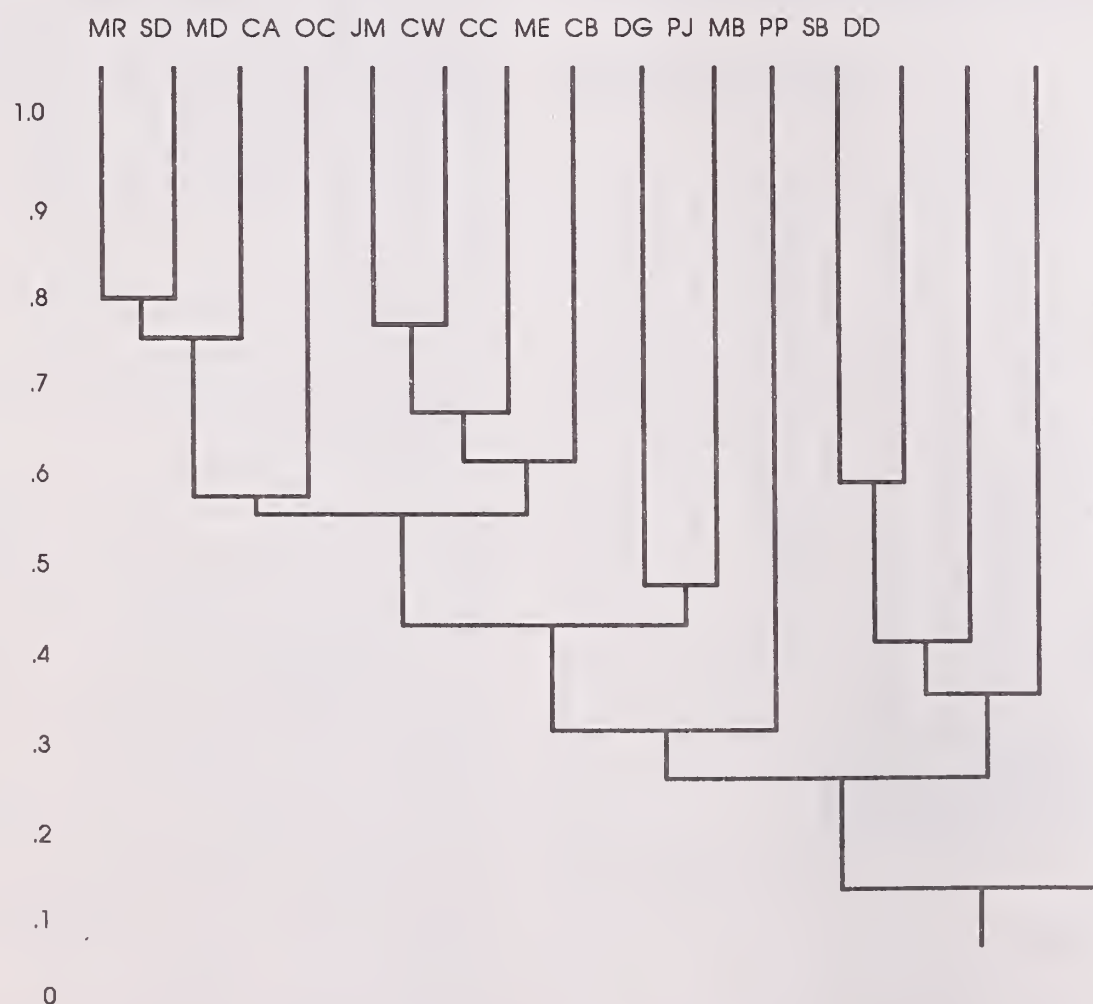


Figure 11.—Cluster analysis (dendrogram) of all data illustrating similarities in habitat type herpetofaunas. (Abbrev. correspond to those listed for habitats in table 1.)

of downed litter (primarily leaves and logs) because of its low preferred body temperature and feeding habits (Jones 1981b, Jones and Glinski 1985). Large amounts of surface litter on certain riparian sites may explain the occurrence of this lizard in cottonwood-willow riparian sites within desert regions (down to 549 m or 1800 ft) (see Jones and Glinski 1985). Several other species typically found on upland habitats (e.g., chaparral), such as *Tantilla hobartsmithii*, *Cophosaurus texana*, *Masticophis bilineatus*, and *Diadophis punctatus*, also may persist on riparian habitats within deserts because of the high moisture regime associated with surface litter, higher humidity, and surface water (Jones and Glinski 1985).

A similar relationship appears to exist in desert habitats occupied by *Xantusia vigilis*. This lizard also has a low preferred body temperature, and it only occurs on Mojave Desert sites occupied by agaves (*Agave* spp.) and yuccas (*Yucca* spp. and *Nolina* spp.); these plants create cool, moist microhabitats within desert habitats. In the southern part of its range, *X. vigilis* only occupies Sonoran Desert on steep slopes in mountain canyons, or on top of mountains (> 1220 m or 4000 ft) in chaparral habitats. This shift in habitat association may reflect increased average temperature and aridity associated with decreasing latitude; canyons and mountain summits may be the only sites moderate enough to support this lizard.

A similar moisture or temperature relationship may also account for differences observed in habitat type associations of *Tantilla hobartsmithii*, *Cophosaurus texana*, and *Diadophis punctatus* in the eastern and western portions of their ranges. In the western portion of the study area, these reptiles occur only in chaparral or riparian habitat types (excluding mixed riparian scrub habitats). In the eastern and southeastern portions of the study area, these species also occur in the Sonoran Desert habitat type. Eastern and southeastern Sono-

ran Desert habitats within the study area are more extensive than those to the west and northwest, and they are not interrupted by large creosotebush habitats; western and northwestern sites are restricted mostly to mountain slopes, separated by extensive creosotebush flats. In addition, eastern and southeastern sites appear to have more springs and perennial creeks than western and northwestern sites, and this additional moisture might contribute to the presence of these species on these sites.

The presence of surface water also has a profound affect on the distribution and abundance of certain species within the study area. *Kinosternon sonoriense*, *Trionyx spiniferus*, *Thamnophis cyrtopsis*, *Bufo alvarius*, *Bufo microscaphus*, *Bufo woodhousei*, *Rana pipiens*, *Rana catesbeiana*, *Hyla arenicolor*, and *Ambystoma tigrinum* occur only on sites with permanent water (springs, creeks, rivers, dirt tanks). All of these species are restricted to permanently watered sites because of a combination of physiological (Walker and Whitford 1970), morphological (Mayhew 1968), reproductive (Justus et al. 1977), or behavioral (Hulse 1974) limitations. In addition to occurring near permanent water, *Bufo punctatus* also occurs in rock-bound canyons with intermittent water, and *Bufo cognatus*, *B. debilis*, *B. retiformis*, and *Gastrophyrne olivacea* occur on sites with clay and clay-loam soils that accumulate surface water during summer convectional rainstorms. All of these species possess adaptations, such as a rapidly developing embryo, that are conducive to survival in areas with intermittent surface water (Creusere and Whitford 1976).

A number of species were verified on fewer than half of the array sites within habitat types. These low percentages may reflect species' association with specific microhabitats and the abundance and distribution of microhabitats within habitat types. For example, *Chilomeniscus cinctus*

occurred on less than half of the cottonwood-willow and mixed riparian scrub array sites. The habitat analysis shows that this species is associated with sandy and fine gravel soils, but many of the cottonwood-willow riparian and mixed riparian scrub sample sites have rocky substrates. Therefore, the substrate type limits this species' range within these habitat types.

However, there were other species, especially snakes in excess of 0.5 m (1.5 ft), that were not readily caught in pit-fall traps, although a small percentage of arrays captured a few large snakes; these snakes were feeding on small rodents at the bottom of traps. Therefore, the paucity of large snakes on sample sites within habitats probably reflects the ability of larger snakes to escape from pit-fall traps rather than the distribution and abundance of microhabitats within habitat types. Additionally, amphibians and reptiles with restricted activity patterns (e.g., toads) or home ranges (*Xantusia vigilis*) also were rarely trapped and, therefore, verified on few sites within a habitat. The limited number of mixed broadleaf and chaparral array sites with *Gerrhonotus kingi* probably reflect a low sampling effort in these habitats during the fall; this lizard's peak activity is during its breeding season in the fall (Robert Bowker personal comm.).

Habitat Conditions

The condition of habitats may play an important role in determining the distribution and abundance of amphibians and reptiles. In Arizona, the large variety of land uses within the area may affect the distribution and abundance of certain microhabitats and may account for variation in species composition within habitats. A number of studies have shown the effects of land uses on amphibians and reptiles and their habitats. These include grazing (Bury and Busack

1974, Jones 1981a, Szaro et al. 1985), off-road vehicle use (Bury et al. 1977, Bury 1980), forest management (Bennett et al. 1980), and stream modification resulting from water impoundments (Jones, this volume). Generally, these affect habitat structure. For example, excessive, long-term livestock grazing reduces the abundance and diversity of forbs and perennial grasses. Many former desert grassland habitats are now dominated by shrubs such as creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) (York and Dick-Peddie 1969). Jones (1981a) showed large differences in the presence and abundance of certain lizards on heavily vs. lightly grazed sites, especially on riparian, desert grassland, and woodland habitats, attributable to differences in lizard ecology and differences in habitat structure between heavily vs. lightly grazed areas. Certain lizards, such as *Cnemidophorus tigris*, prefer open, shrubby sites; these lizards are more abundant on heavily grazed sites where shrubs have replaced grasses and forbs (Jones 1981a). Conversely, certain lizards, such as *Eumeces gilberti*, prefer grassy, moist sites, and are, therefore, less abundant on or absent from sites where grazing has reduced tree reproduction (e.g., cottonwoods, *Populus fremontii* on riparian sites) or suppressed grasses (e.g., on desert grassland sites) (Jones 1981a).

The reduction of naturally-occurring water and the modification of river and stream habitats has been shown to affect the composition of amphibians and reptiles within habitats, especially riparian sites (Jones 1988). Platz (1984) attributes the extinction of *Rana onca* to modification of stream habitats along the Virgin River. Species that prefer lentic or pool habitats should increase on sites with water impoundments, whereas species that prefer lotic or running water should decrease.

Natural phenomena, such as fire, also affect species composition within habitats (Kahn 1960, Simovich

1979). Simovich (1979) showed that fire set back succession within chaparral habitats (grass/forb successional stage), and that these changes resulted in increases in certain species and decreases in others. As succession proceeded to shrubs and trees, reptiles that were abundant in the grass/forb successional stage (e.g., *Phrynosoma coronatum*) became less abundant, and others that preferred wooded sites (e.g., *Sceloporus occidentalis*) became more abundant.

Historical vs. Present Distributions

Prior to this study, records of amphibians and reptiles on the study area were limited; one of the primary reasons for which this study was conducted was to assemble basic distribution information. Therefore, range expansions or reductions were hard to document. This study resulted in range extensions of approximately 35 species, and clarified the relationship of Arizona habitats to habitats in adjacent geographic regions. Many species, such as *Heloderma suspectum*, *Eumeces gilberti*, *Sceloporus clarki*, *Tantilla hobartsmithii*, and parthenogenic whiptail lizards (*Cnemidophorus flagellicaudus*, *C. uniparens*, and *C. velox*) proved to be considerably more widespread than previous records indicated—not surprising since many areas had never been intensively sampled. The expansion of *E. gilberti*'s range results from the discovery of the California subspecies, *E. g. rubricaudatus*, in chaparral and pinyon-juniper habitats; the distribution of *E. g. arizonensis* is limited to a cottonwood-willow riparian habitat along an 18 km (11 mi) stretch of the Hasayampa River immediately south of Wickenburg (see Jones et al. 1985, Jones and Glinski 1985).

Only one species demonstrated a range reduction. Pure populations of *Bufo microscaphus* have apparently been reduced due to hybridization with *Bufo woodhousei*, especially on

major drainages. Water impoundment and diversion-associated changes in aquatic habitats from permanent riffles and runs to pools may have caused the immigration of *B. woodhousei* into areas formerly occupied by only *B. microscaphus* (Brian Sullivan personal comm.).

There is considerable taxonomic confusion about a population of *Kinosternon sonoriense* on the Big Sandy River near Wikieup. Because specimens with raised 9th marginal scales had been taken from this area, Stebbins (1966) considered this population to be *Kinosternon flavescens*, but Iverson (1978) considered it to be *K. sonoriense*, based on specimens without 9th marginals. Of the 12 individuals observed during this study, 6 had raised 9th marginals and 6 did not. Based on its large separation from the nearest population of *K. flavescens*, Iverson (personal comm.) considers this population to be an aberrant form of *K. sonoriense*.

Similarity of Habitats Types

It is possible to discern definite patterns in the diversity of and similarities between the herpetofaunas of different habitat types within the study area. There is an apparent elevational gradient affecting species diversity. Desert habitats between 610 and 1067 m (2000-3500 ft), riparian habitats between 549 and 1220 m (1800-4000 ft), and chaparral habitats between 1067 and 1525 m (3500-5000 ft) had greater species richness than higher elevation woodland (> 1677 m or 5500 ft, e.g., Ponderosa pine) and desert habitats (> 1220 m or 4000 ft, e.g., sagebrush). Additionally, low elevation desert habitats (> 610 m or 2000 ft, e.g., creosotebush), had relatively low species diversity. Higher species diversity on middle elevation habitat types may reflect these habitats' moderate environmental and climatic conditions, whereas higher and lower elevation habitats possess

extreme environmental and climatic conditions (e.g., temperature). For example, low elevation creosotebush habitats have sparse canopies, and temperatures often exceed 60 C near the surface in summer (Oosting 1956). High elevation sites are cold and are often snowcovered until late April so that the growing season is short. Although possessing relatively low species richness, low elevation creosotebush habitats are more diverse than high elevation sites. These differences in diversity may reflect thermal conditions at these elevational extremes. Many of the species that occur within creosotebush are nocturnal, and, therefore, these animals avoid exposure to extreme surface heat. On higher elevation habitats, the problem is not avoiding heat but, rather, gaining heat for activity. Other than along rock outcrops, rapid heating is difficult for reptiles at higher elevations. Differences between diversity and species composition on medium elevation habitat types probably reflect differences in microhabitat abundance and diversity on habitat types (see earlier discussion on microhabitats). Lack of diversity on disclimax desert grassland sites probably reflects the lack of vegetation structure on these sites.

There was similarity in the herpetofaunas of certain habitat types. All desert habitats, except sagebrush, had very similar herpetofaunas, as did most moderate elevation habitats (e.g., chaparral, pinyon-juniper, and mixed riparian scrub). This is predictable because all of these habitats occur in close proximity and are structurally similar. There was a moderate degree of similarity between cottonwood-willow riparian and desert habitats, chaparral and cottonwood-willow riparian, and chaparral and desert habitats. Because cottonwood-willow riparian habitats traverse through both desert habitats and upland habitats, many of the species associated with the surrounding habitats also frequent riparian sites; riparian sites are im-

portant sources of food and cover (Ohmart and Anderson 1986). Similarities between chaparral and desert habitat types, such as Mohave Desert, Sonoran Desert, and mixed riparian scrub, result from occurrence of typical desert species (e.g., *Callisaurus draconoides*) on upland sites rather than the occurrence of upland species (e.g., *E. gilberti*) on desert sites.

The diversity of and similarities among amphibian and reptile communities of habitat types also may have been affected by the proximity of habitat types to evolutionary centers. Because of the many new records for herpetofauna generated by this study, we now have a better picture of the sources of diversity for this area. Many of the amphibians and reptiles occurring in the Sonoran and Mohave Deserts evolved in Baja California and along the western section of mainland Mexico; these areas were linked until their separation 13 million years ago (Murphy 1983). With the retreat of pleistocene glaciation and spread of xerophyllous and desert habitats, amphibians and reptiles moved northward into southern California and southwestern Arizona; hence, Sonoran and Mohave Desert habitat types have similar herpetofaunas. Although many species immigrated into what is today the Sonoran and Mohave Deserts, only a few species immigrated as far north as the Great Basin Desert. Higher elevations may have precluded many of these species from colonizing the Great Basin desert habitat types and, hence, it's herpetofauna is different from and less rich than those of the other two deserts.

The discovery of the subspecies *Eumeces gilberti rubricaudatus*, formerly unknown in Arizona, suggests that Arizona chaparral was closely associated with California chaparral during Pleistocene glaciation; *E. g. rubricaudatus* evolved in California sclerophyll woodland (Taylor 1935). That parthenogenic whiptail lizards, such as *Cnemidophorus flagellicaudis*, *C. uniparens*, and *C. velox*, are absent

from California chaparral suggest that these species evolved after Pleistocene glaciation.

There were a few inconsistencies in the results of the two analyses used to determine similarity between habitats (the cluster analysis of all data vs. the cluster analysis of only array data). These inconsistencies partially result from the inconsistency of arrays to capture turtles and medium and large-sized snakes, and partially from the analyses themselves (see the Methods Section for a more detailed explanation).

Conclusions and Recommendations

This survey indicates that most species present within western Arizona are widespread, and that few warrant special management consideration. However, it is evident that certain species are more vulnerable to range or population reduction than others. Generally, these species are those that require microhabitats that are easily affected by land uses.

It appears that habitat moisture and moderated surface temperatures are of primary importance to many species in western Arizona. Downed and dead surface litter (debris), such as logs and leaves, play a major role in moderating surface temperature and enhancing moisture (Daubenmire 1974). Horizontal and vertical vegetation structure also help moderate temperatures and increase moisture. In developing management schemes, priority should be given to maintaining or enhancing surface litter and vegetation structure. It is important to maintain tree reproduction, and to leave litter on the surface rather than piling and burning it. The latter practice is especially important on cottonwood-willow riparian sites within deserts, since many species in riparian sites are totally dependent on surface litter for their survival (Jones and Glinski 1985). Many riparian sites within the study area have

reduced amounts of trees and surface litter, principally because livestock have greatly reduced the reproduction of cottonwood trees by reducing the survival of seedlings (Jones 1981a). Management prescriptions are needed on these sites to increase the survivorship of seedling and young cottonwood trees.

Populations of "upland" species (e.g., *Eumeces gilberti*) on habitat islands are more vulnerable to impacts associated with certain land uses than populations occurring on major, continuous stands. Jones et al. (1985) described these habitat islands, some only 10 ha (25 acres) in size. Loss or fragmentation of any portion of these islands could result in the local extirpation of one or several upland species (see Bury and Luckenbach 1983 and Harris 1984 for the effects of habitat fragmentation and habitat loss on species occurring on habitat islands). Because even small modifications to island habitats can result in the extirpation of upland species, proposed projects should be moved to alternative sites whenever possible; mitigation strategies should be used only as a last resort. Top priority should be given to protecting these sites in land-use and on-the-ground activity plans (see Jones et al. 1985 for specific locations of these sites).

Although all amphibians in the study area (excluding *Bufo microscaphus*) appear to be stable, water in many habitats continues to be developed. In addition, new information (Bruce Bury personal comm, Corn and Fogleman 1984) suggest that several populations of ranid frogs have been extirpated from western North America, although there is no apparent cause for their extirpation. Considering the heavy use of spring and creek water, and the reported loss of many ranid populations in the West, high priority should be given to monitoring amphibian populations at springs and creeks in Arizona. Additionally, high priority should be given to de-

termining the extent of hybridization between the toads *B. microscaphus* and *Bufo woodhousei*. Pure populations of *B. microscaphus* should be located and protected against hybridization with *B. woodhousei*. If only a few pure populations are found, the Arizona Game and Fish Department and/or the U.S. Fish and Wildlife Service should set up a captive breeding program to reduce this toad's risk of extinction.

Although I obtained distributional records of *Gopherus agassizii*, Burge (1979, 1980) and Schneider (1980) provide considerably more detail on the needs of this species. However, many biologists consider *G. agassizii* to be declining throughout most of its range. The U.S. Fish and Wildlife Service (1987) continues to list *G. agassizii* as a species that needs further study to determine its status, although it has determined that the Federal listing of the tortoise throughout its range is warranted but precluded by species needing more immediate listing (e.g., species in more eminent danger of extinctions). The BLM should continue to give high priority to the study and management of this species in Arizona.

If the few measures suggested in this paper are implemented, western Arizona should continue to support one of North America's most diverse herpetofaunas.

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Multivariate Analysis of the Summer Habitat Structure of *Rana pipiens* Schreber, in Lac Saint Pierre (Québec, Canada)¹

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The leopard frog, *Rana pipiens*, is the most abundant frog species in the Lac Saint Pierre area (Leclair 1985, Leclair and Baribeau 1982, Paquin 1982), and also one of the most common vertebrates in aquatic communities in North America (Dole 1965a). Despite this apparent abundance, many herpetological surveys made in the last fifteen years have shown dramatic reductions in leopard frog densities. Gibbs et al. (1971) estimated a 50% drop in the global population of leopard frogs in the USA, during the 1960's. Many other workers have reported population reductions and local extinctions in Canada and the USA (Collins and Wilbur 1979, Cook 1984, Degraaf and Rudis 1983, Froom 1982, Hayes and Jennings 1986, Hine et al. 1981).

In area where hypothesis of predation or competition by introduced species (Bullfrogs or predatory fishes) (Hayes and Jennings 1986) does not apply, two major causes have been invoked as responsible for

this situation (1) overexploitation of natural stocks, and (2) loss or alteration of habitat rendering it unsuitable for *R. pipiens* (Cook 1984, Frier and Zappalorti 1984, Leclair 1985, Marcotte 1981, Rittschof 1975). Riparian habitats have been especially affected by human activities (Sarrazin et al. 1983, MLCP 1985). In Canada, 50% of the wetlands that once supported wildlife have now been reclaimed for agricultural, industrial or urban development, or have been altered by pollution (SCF 1980). Even greater riparian habitat has occurred along the St. Lawrence river, where 70% of the riparian habitats have been eliminated.

According to Ministère des Loisirs, de la Chasse et de la Pêche (MLCP) (1985), essential habitats are those vital to population or species survival, whether these habitats are used temporarily or permanently. This definition emphasizes several crucial aspects of amphibian habitat use, i.e. the use of aquatic as well as terrestrial habitats, and of migratory routes between the two. Up to now, quantitative studies of habitat requirements for anuran species have focused mostly on the aquatic habitats (Beebe 1977, Clark and Euler 1982, Dale et al. 1984, Gascon and Planas 1986, Hine et al. 1981). This situation largely results from the lack of appropriate quantitative sampling method for amphibian populations in terrestrial habitats (Bury and Raphael 1983, Clawson et al. 1984). Recently,

Abstract.—Thirty stations representing various riparian habitats typical of the Lac Saint Pierre area were sampled with a system of drift fences and funnel traps to characterize the summer habitat structure of a leopard frog population. A discriminant analysis indicates that habitats with high frog density (1) are close to the marsh line, (2) have a tall herbaceous stratum with high richness and (3) have a low moss cover. A stepwise multiple regression model used 5 of the vegetation structure variables, and explains ca. 70% of the variability associated with frog density among stations.

Campbell and Christman (1982), and Vogt and Hine (1982) have developed adequate techniques that help overcome this situation.

The aims of the present study were (1) to characterize the structural aspects (biotic and abiotic) of the terrestrial habitats of *Rana pipiens* and (2) to develop a model relating frog abundance to habitat descriptors.

Study Area

The study area is a 30 X 0.9 km strip extending from Trois-Rivières to Berthierville (Québec, Canada), on the north shore of Lac Saint Pierre (73°30' W X 46°05' N). The Lac Saint Pierre covers about 300 km² and is formed by a widening of the St. Lawrence river (fig. 1). The lake flood plain is extensive (Tessier et al. 1984) and consequently, spawning sites for amphibians are abundant in spring. The habitats most frequently used by *Rana pipiens* (based on mating call frequencies) are flooded fields of reed phalaris (*Phalaris arundinacea*) and of purple loosestrife (*Lythrum salicaria*), mixed with willow (*Salix* sp.) (Leclair 1983). From these fields, numerous bays, small rivers, draining canals and natural or man-made pools facilitate movement of frog towards adjacent terrestrial habitats.

According to the maps produced by Denis Jacques (1986) and by Tessier and Caron (1980) on the riparian vegetation of Lac Saint Pierre,

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at least ten plant communities may be recognized on the criterion of dominant species. These plant communities can be grouped in six different physiognomic types (table 1). Thirty stations were selected in order to sample the diversity of habitats. From the maps, sampling sites were located in habitat patches not having less than 2500 m² of homogeneous vegetation. The final choice of sites was determined by physical and legal accessibility.

Materials and Methods

Sampling Technique

At each station, frogs were sampled with 12 funnel traps placed on each side of two 15 m drift fences made of polyethylene and forming a right angle (fig. 2). Dirt and/or litter was brushed into the mouth of each funnel to simulate a natural entrance

(Clawson and Baskett 1982). This design has been shown to allow for sampling in various kinds of terrestrial habitats, and to provide data for the estimation of demographic parameters and for comparison between various habitats (Campbell and Christman 1982, Clawson et al. 1984).

Funnel traps were opened for at least 10 consecutive days in each period (10 days in May, 10 in June, 12 in July, 10 in August, 22 in Fall) and were checked every other day.

Data recorded for each capture were: date, station number, direction of capture (N, S, E or W), species, sex and snout-urostyle length. Captured frogs were marked by clipping the fourth digit of the hindfoot. Clipped phalanges were kept for age determination through skeletochronological examination (Leclair and Castanet 1987).

Because of the way the arrays were used for sampling, captures reflected the relative abundance of frogs among stations, not their absolute density.

Environmental Variables⁴

Each station was characterized by 6 spatial variables: distance to the marsh line (DMARSH), to the nearest permanent pool (DWATERP), to the nearest temporary pool (DWATER⁵),

⁴See appendix 1 for all abbreviations used in the text.

⁵Variable measured monthly.

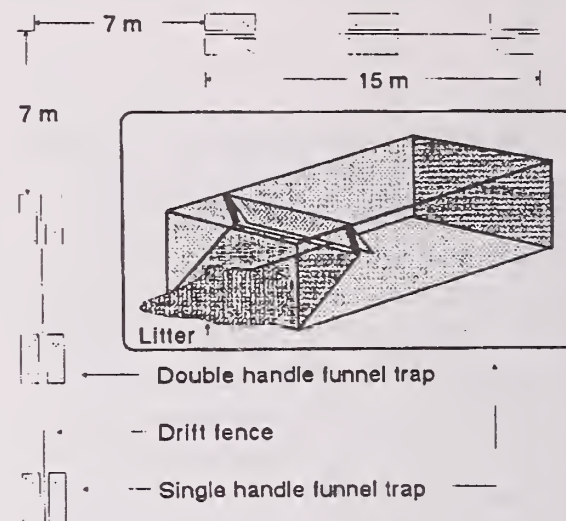


Figure 2.—Schematic representation of the trapping arrays.

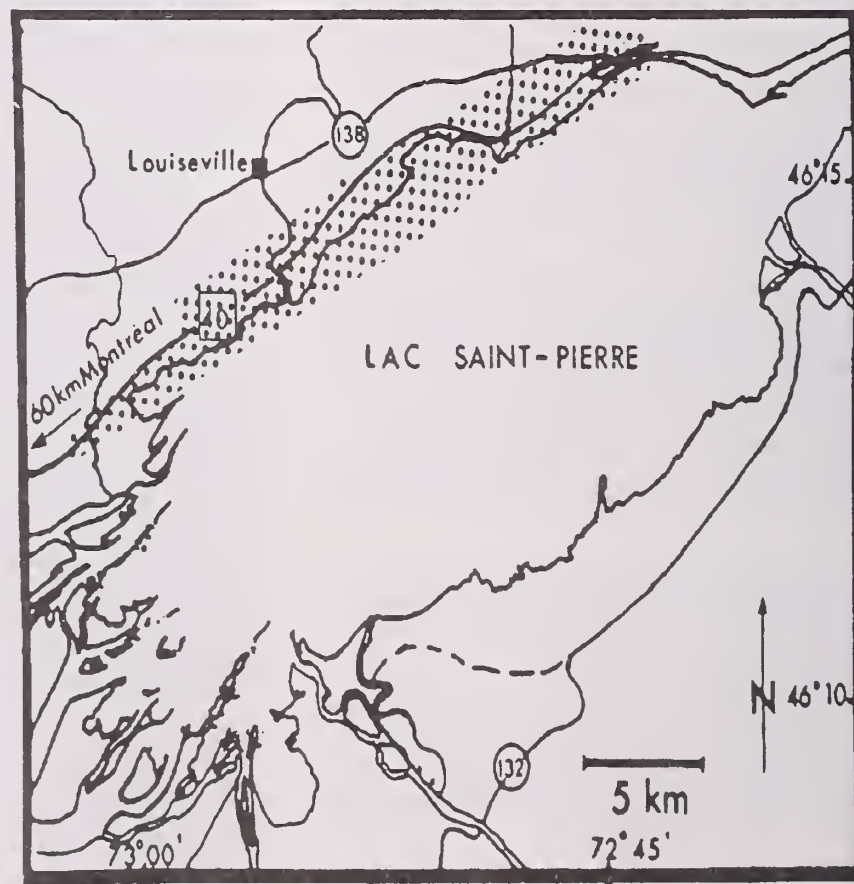


Figure 1.—General location of the study area (upper map) and the study area's relationship to lake St. Pierre (Quebec, Canada) (lower map).

to the nearest human alteration (road, path, residence, crop) (DHUMAN), and to the nearest open habitat without shrub or tree canopy (DOPEN) or closed habitat with canopy (DCLOSE). All distances were measured in the field with a toposil marker (lost thread measure apparatus), except for some measures of DMARSH taken from a 1:10 000 topographical map. Elevation from the

marsh ground (ALTREL) was taken with a Keuffel and Essel altimeter. Water table level (WTABLE⁵) was measured with a piezometer, placed 1 m deep.

Edaphic variables measured were: soil moisture (MOIST⁵), from oven-dried soil samples (80°C, 24 hrs); soil fractions (SAND, SILT, CLAY), as determined by the Bouyoucos method (Bouyoucos 1936); soil water

pH (PH), as determined with a Fisher pH-meter, and soil temperature (TEMP2). The soil temperature variable used in the statistics is expressed as the sum (5 reading per month) of the deviations from the daily mean taken over all stations.

Percent of ground covered by litter (LITTER⁵), dead wood (DEADWOOD), mosses (MOSSCOV⁵), herbaceous plants (HERBCOV⁵), and percent bare ground (BAREGRND⁵) was estimated by two independent observers in 5 X 5 meters quadrat, and the mean was recorded. Litter thickness (LITTHICK⁵) and height of the herbaceous stratum (HERBHIGHT⁵) represented the mean of 5 measurements taken with a meterstick.

Quantitative assessment of vegetation structure was represented by Fox's photometric index (Fox 1979) as:

$$V_x = \frac{\ln(Ia/Ib)}{H(b-a)}$$

where V_x represents the photometric index for the amount of vegetation present in a layer between two levels, when Ia and Ib are the light intensities immediately above and below the layer and $H(b-a)$, the layer thickness. Readings of light intensity were taken with a Sekonic light meter, at 0, 20, 50, and 100 cm above ground, above the herbaceous canopy and in the open field adjacent to station having closed canopy. At each site, measurements were taken at five points which were then averaged to provide one value. Five photometric index were computed: vegetation index in the 0-20 cm layer (PHOT20⁵); from 20 to 50 cm (PHOT50⁵); from 50 to 100 cm (PHOT100⁵); herb layer above 100 cm (PHOT+⁵); and shrub and tree strata (PHOTCAN⁵).

Vegetation structure was also described in 8 growth-form categories: (TREE) woody plants > 10 cm diameter; (SHRUBHI) woody plants > 2.5 m tall; (SHRUBLO) woody plants < 2.5 m tall; (HGH⁵) high graminoid herbs > 100 cm tall; (MGH⁵) medium

Table 1.—Characteristics of the sampling stations according to physiognomic type and to major plant species.

Sta.	Physiognomic type	Code	Major plant species
1	Open dry field	O	<i>Solidago canadensis</i> , <i>Aster umbellatus</i>
2	Brushy dry field	B	<i>Spirea latifolia</i> , <i>Populus tremuloides</i>
3	Wooded swamp	F	<i>Acer saccharinum</i> , <i>Laportea canadensis</i>
4	Riparian marsh	M	<i>Sparganium eurycarpum</i> , <i>Scirpus fluviatilis</i>
5	Shrub swamp	S	<i>Spirea latifolia</i> , <i>Onoclea sensibilis</i>
6	Wet prairie	P	<i>Calamagrostis canadensis</i> , <i>Phalaris arundinacea</i>
7	Open dry field	O	<i>Solidago rugosa</i> , <i>Aster umbellatus</i>
8	Wooded swamp	F	<i>Acer saccharinum</i> , <i>Laportea canadensis</i>
9	Wet prairie	P	<i>Carex lacustris</i> , <i>Lythrum salicaria</i>
10	Wooded swamp	F	<i>Salix nigra</i> , <i>Laportea canadensis</i>
11	Wet prairie	P	<i>Typha latifolia</i> , <i>Onoclea sensibilis</i>
12	Shrub swamp	S	<i>Salix</i> spp., <i>Myrica gale</i>
13	Wet prairie	P	<i>Calamagrostis canadensis</i>
14	Shrub swamp	S	<i>Salix cordata</i> , <i>Phalaris arundinacea</i>
15	Riparian marsh	M	<i>Sparganium eurycarpum</i> , <i>Equisetum fluviatile</i>
16	Wet prairie	P	<i>Phalaris arundinacea</i>
17	Brushy dry field	B	<i>Spirea latifolia</i> , <i>Populus tremuloides</i>
18	Wet prairie	P	<i>Carex lacustris</i> , <i>Lythrum salicaria</i>
19	Brushy dry field	B	<i>Spirea latifolia</i> , <i>Salix</i> spp.
20	Open dry field	O	<i>Solidago canadensis</i> , <i>Aster umbellatus</i>
21	Open dry field	O	<i>Phleum pratense</i> , <i>Agrostis alba</i>
22	Wet prairie	P	<i>Calamagrostis canadensis</i> , <i>Phalaris arundinacea</i>
23	Shrub swamp	S	<i>Salix</i> spp., <i>Rorippa amphibia</i>
24	Riparian marsh	M	<i>Sparganium eurycarpum</i> , <i>Sagittaria latifolia</i>
25	Wooded swamp	F	<i>Acer saccharinum</i> , <i>Populus deltoides</i>
26	Shrub swamp	S	<i>Salix</i> spp., <i>Spirea latifolia</i>
27	Wooded swamp	F	<i>Acer saccharinum</i> , <i>Onoclea sensibilis</i>
28	Riparian marsh	M	<i>Sparganium eurycarpum</i> , <i>Rorippa amphibia</i>
29	Wet prairie	P	<i>Carex lacustris</i> , <i>Lythrum salicaria</i>
30	Wet prairie	P	<i>Calamagrostis canadensis</i> , <i>Lythrum salicaria</i>

size graminoid herbs from 20 to 100 cm tall; (HBLH⁵) high broad-leaf herbs > 100 cm tall; (MBLH⁵) medium size broad-leaf herbs from 20 to 100 cm tall; (SMALL⁵) herbs layer below 20 cm tall. Basal area (BA-SAREA) was calculated by measuring tree diameter at breast height with a caliper. Richness in herbs species (NSPHERB), shrubs (NSPSHRUB), and trees (NSPTREE) was determined in a 400 m² quadrat. Minimal area of homogeneous vegetation patch (MINAREA) was estimated according to the graphical method of Braun-Blanquet (1964).

Statistics

Spearman rank correlations and chi-square tests were used to test for non-random distribution of captured frogs among age class and among periods of sampling. Chi-square tests were also used to detect a significant movement of frogs. Because some variables were not normally distributed (Kolmogorov-Smirnov test), they were square-root transformed before analysis (indicated on appendix 1).

For final analyses, the number of variables was reduced by screening an initial principal component analysis (PCA), and by using Pearson rank correlations (Green 1979). Because of heterogeneity in the variables measured, the correlation matrix was used to extract the principal components that explained the greatest proportion of variability. A second PCA with the 22 extracted variables served to define the structural differences among stations, and to reduce the data set to a few important dimensions that could identify most of the structural variability among measured habitats. To construct a classification model for potential habitats, a discriminant analysis (DFA) was done on three groupings of stations based on frog abundance. The model was validated through a simulation.

A stepwise multiple regression was used to identify which habitat characteristics account for most of the variability in the analyzed data (Clawson et al. 1984). An independent variable was included in the model when its partial F-value was significant ($\alpha = 0.05$). Partial correlation coefficients were used to verify the statistical relation between the dependent variables and the independent one. This analysis has been identified as the most appropriate to study the combined effects of various

habitat variables on wildlife density (Legendre and Legendre 1984). Interpretation of the models obtained from such analyses takes into account combinations of variables, but not variables taken individually (Scherrer 1984). Statistical analyses were performed with SPSS (Nie et al. 1975).

Results

A total of 798 individuals representing 4 species of anurans (*Rana pipiens*,

Table 2.—Capture data by sampling period, and by age class.

Station	Number of captures								Sum	Sum ² adjusted
	By month					By age class				
	M	J	J	A	S-O	Adult	Juv.	NMY ¹		
1	0	1	0	2	2	4	0	1	5	5
2	0	0	3	2	6	5	3	3	11	11
3	1	0	0	1	3	2	2	1	5	5
4	8	11	5	3	7	11	17	6	34	34
5	6	3	4	2	2	15	1	1	17	17
6	7	13	3	3	9	20	11	4	35	35
7	0	1	1	3	1	5	0	1	6	6
8	0	0	1	0	2	0	2	1	3	3
9	8	8	4	2	5	14	7	6	27	27
10	3	9	3	2	2	12	3	4	19	19
11	5	3	1	2	8	7	4	8	19	19
12	11	9	4	4	3	21	3	7	31	31
13	15	8	7	12	5	28	13	4	47	47
14		22	7	10	39	47	16	12	78	107
15	12	15	8	12	39	51	21	11	86	86
16		3	0	2	0	3	1	1	5	7
17	0	0	0	0	0	0	0	0	0	0
18		0	0	0	0	0	0	0	0	0
19	0	0	3	0	0	3	0	0	3	3
20	0	0	0	0	0	0	0	0	0	0
21	0	0	3	1	1	0	0	5	5	5
22	5	2	6	2	0	8	4	0	15	15
23	10	10	2	1	0	9	13	0	23	23
24	26	21	3	2	7	28	23	1	59	59
25	8	3	1	4	3	17	2	0	19	19
26	5	1	1	3	7	12	1	3	17	17
27		0	1	4	9	6	3	5	14	19
28		2	10	12	10	20	3	11	34	47
29	5	2	0	1	1	3	5	0	9	9
30		3	5	6	7	11	3	7	21	29
Total	135	150	86	98	178	362	161	103	647	704

¹Newly metamorphosed young.

²Sum adjusted for stations not inventoried in May.

R. catesbeiana, *R. sylvatica*, *Bufo americanus*) were captured during the study. Many small rodents ($n = 188$) and a few weasels (*Mustela erminea*) were also captured. The results presented here relate only to *R. pipiens*.

Table 2 presents the capture data for the various stations and sampling periods, along with data on population age structure. The mean capture rate is 0.35 capture/day/station; stations range from 0 to 1.77 captures/

day/station. Preliminary trials on three stations in fall 1986 had given 4.8 captures/day/station.

Spearman's correlation coefficients (table 3) from among all possible age groups and sampling period pairs were all significant except those between captures at period 1 and newly metamorphosed young ($R = 0.3471$, $P = 0.097$). We also compute a contingency table (table 4) to check for independence of the two vari-

ables "age group" and "physionomic type of habitat." There was a weak relationship ($D.F. = 8$, $X^2 = 16.64$, $0.025 < P < 0.5$) created mostly by the capture of a few young ($n = 5$) at a dry open field station (# 21, see table 2). Otherwise, all other habitats shared proportional distribution for the different age groups ($D.F. = 6$, $X^2 = 8.04$, $0.10 < P < 0.25$). Further general PCA and DFA models used the number of total captures per station, irrespective of sampling periods or age groups.

Following preliminary screening, we removed variables that were not normally distributed (DOPEN, DCLOSE, DEADWOOD, HBLH, SMALLH), those correlated with other variables (DWATERP, LITTER, SAND, WTABLE), and those related to the tree and shrub strata (NSPTREE, NSPSHRUB, TREE, SHRUBHI, SHRUBLO, BASAREA, PHOTCAN) which diluted the results of PCA.

Figure 3 illustrates the distribution of the remaining 22 variables along the first two PCA axes, based on data of table 5. The first axis explains 22.3% of the variation and is correlated to descriptors of vegetation structure, such as density of graminoids (HGH), vegetation height (HERBHGHT), photometric index

Table 3.—Spearman rank correlations and significance level between captures for all possible age groups and sampling periods pairs.

Period/Age	Periods					Age		
	M	J	J	A	S-O	Adult	Juv	NMY ¹
May	—	***	**	***	**	***	***	NS
June	0.88	—	***	***	**	***	***	*
July	0.59	0.57	—	***	**	***	***	***
August	0.63	0.56	0.64	—	***	***	**	***
Sep.-Oct.	0.52	0.47	0.52	0.75	—	***	***	***
Adult	0.88	0.83	0.74	0.81	0.67	—	***	***
Juvenile	0.82	0.79	0.59	0.49	0.60	0.70	—	*
NMY1	0.35	0.44	0.62	0.70	0.81	0.56	0.46	—

¹Newly metamorphosed youngs.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

NS = non significant.

Table 4.—Contingency table for non random distribution of age group captures among the physionomic types of habitat.

Age groups	Physionomic types of habitat					
	Dry habitat ¹	Shrub swamp	Wooded swamp	Wet prairie	Riparian marsh	
NMY	10	23	11	30	29	Count
	4.9	26.5	9.9	28.3	33.4	Exp. val.
Juvenile	3	34	12	48	64	Count
	7.7	41.4	15.4	44.2	52.2	Exp. val.
Adult	17	104	37	94	110	Count
	17.3	93.1	34.7	99.5	117.4	Exp. val.

For all habitats: $D.F. = 8$, $X^2 = 16.64$, $0.025 < P < 0.05$.

Without dry habitats: $D.F. = 6$, $X^2 = 8.04$, $0.10 < P < 0.25$.

¹Open dry field and Brushy dry field were joined to respect chi-square requirements.

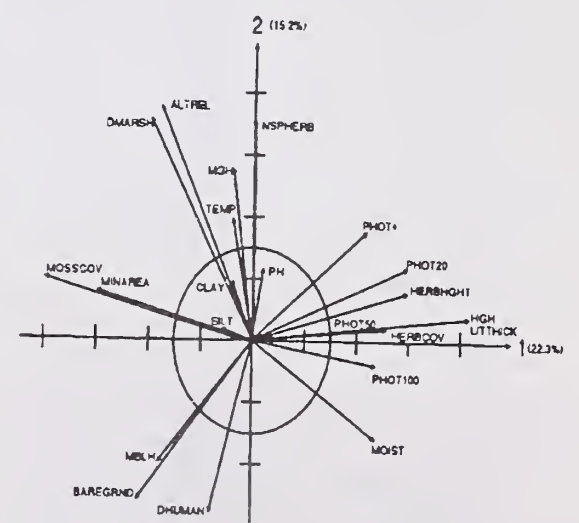


Figure 3.—Projection of the 22 biophysical variable vectors onto plane defined by the first two principal components. The circle at the origin has a radius of 0.30.

(PHOT20, PHOT+), litter thickness (LITTHICK) and moss cover (MOSSCOV). The second axis explains 15.2% of the variability and is correlated to marsh distance (DMARSH, ALTREL), number of herb species (NSPHERB), mid-height graminoids (MGH), short distance to human alteration (DHUMAN) and bare ground (BAREGRND). The third axis explains 10.5% of the data variability, which is significant according to the broken stick model (Frontier 1976, Legendre et Legendre 1984). It is related to edaphic factors such as: pH (PH), silt fraction (SILT) and soil moisture (MOIST) (table 5). The forth and subsequent axes are not significant.

Figure 4a gives the relative position of stations according to the first two axes of the PCA. Five groups

may be easily circled at best, according to their physionomic type. Dry habitats (open and brushy fields) are at the top of the figure and are characterized by a greater distance to the marsh line, a higher moss cover and a plant cover which is meager but has a high species diversity. The dry open fields with high PHOT+ are distinct from the dry brushy fields which have a lot of bare ground, those two variables being in opposite direction (fig. 3). Although the variables on tree and shrub strata were removed from PCA, wooded and shrub swamps appear distinct from the other habitats. They are clustered along the BAREGRND and MBLH vectors (fig. 3) opposed to variables describing vegetation structure and positively correlated to the first axe. Wet prairies and riparian marshes

can be differentiated from the other three habitats along the first axis by a more elaborated herbaceous structure. Stations positioned in the *Spartanium eurycarpum* community, which occupies approximately the first 100 m of the riparian marsh (Tessier et al. 1984), have a very wet soil, the water receding only about the end of May. Wet prairies are distinguished from the preceding habitat by the conjugated differences of many variables related to axe 2.

Figure 4b shows the position of the stations as in figure 4a but are best circled by classes of frog abundance. This figure emphasizes the relationship between habitat aridity and frog density, the lowest frog densities occurring in the driest habitats (open dry field, brushy dry field). Higher frog density stations include those from the marsh line and those from the wet fields. Intermediate frog densities occur in forest and shrub sites.

A DFA of frog density classes allowed us to identify a few variables that were easy to quantify and also to classify habitats according to their potential use by leopard frogs. Table 6 presents the standardized coefficients (computed with z-score) of the variables for each DFA axis, and non-standardized coefficients associated with classification function. Four such variables were retained from DFA. DMARSH alone allows for 60% of the stations to be correctly classified. Addition of the NSPHERB variable adds another 13%. When PHOT+ and MOSSCOV variables were used, 90% of the stations were correctly classified.

Figure 5 integrates information about habitat and density by indicating the position of each station and group centroids of frog density classes along the two canonical axes. As for PCA, the value of the standardized coefficients for each variable associated to each DFA axis is proportional to the length of each arrow. The first axis, which represents the major part of the interclass vari-

Table 5.—Sorted factor loadings for the principal component analysis of habitat variables.

	Factor		
	1 (22.3%) ¹	2 (15.2%)	3 (10.5%)
HGH	0.845	0.094	0.271
LITTHICK	0.841	0.102	-0.119
MOSSCOV	-0.772	0.180	0.139
HERBHGT	0.604	0.144	0.178
MINAREA	-0.602	0.158	0.184
PHOT20	0.586	0.266	-0.016
HERBCOV	0.536	0.040	-0.413
PHOT+	0.845	0.400	0.250
ALTREL	-0.347	0.753	0.087
DMARSH	-0.394	0.738	-0.166
NSPHERB	-0.006	0.654	0.464
MGH	-0.067	0.578	-0.125
DHUMAN	-0.146	-0.566	0.050
BAREGRND	-0.444	-0.537	0.143
SILT	-0.098	0.042	0.696
PH	0.097	0.264	-0.640
MOIST	0.481	-0.313	0.509
TEMP	-0.108	0.404	-0.208
PHOT100	0.490	-0.090	-0.384
PHOT50	0.452	0.030	0.409
MBLH	-0.337	-0.405	-0.077
CLAY	-0.088	0.214	0.314

¹Percentage of total variance explained by each component.

ability (88.8%), is mostly related to DMARSH, NSPHERB and MOSSCOV. The second axis (11.2% of intergroup variation) reflects primarily variation in the photometric index above 1 m (PHOT+) and NSPHERB.

To validate our discriminant model, we randomly drew 103 samples of three groups of stations, and ran a DFA. The distribution of the 103 samples does not depart significantly from normality (Kolmogorow-Smirnov test = 1.233, $P = 0.096$). The results give a mean of correct classifications of 68.6% with a maximum of 83.3% and a standard error of 7.2%. A t-test ($T = 2.98$, $P(1) = 0.0025$) indicates that the probability of obtaining a value equal to 90% is less than 0.0025.

Finally, using stepwise multiple regression analyses, we identified those variables used in models that best predict frog abundance. For such modelling, Clawson et al. (1984) have pointed out the importance of

Table 6.—Summary statistics for discriminant function analysis of habitat characteristics according to three classes of frog abundance (as defined in fig. 4b).

Variable	Wilk's lambda	P	% correct classification total	Standardized coefficients ¹		Unstandardized coefficients ²	
				Axe 1 88.8 %	Axe 2 11.2 %	Axe 1	Axe 2
DMARSH	0.505	0.0001	60.0	1.220	0.065	0.00613	0.00033
NSPHERB	0.328	<0.0001	73.3	-1.024	0.505	-0.143	0.071
PHOT+	0.255	<0.0001	73.3	0.537	0.709	0.584	0.771
MOSSCOV _N	0.214	<0.0001	90.0	0.500	-0.185	0.480	-0.179
(CONSTANT)						-0.908	-1.522

¹DFA uses z-score data and gives the relative contribution of each variable to final discrimination.

²Classification function uses original data and allows to know to which group sampling stations belong. DMARSH expressed in meter, NSPHERB expressed in number of herb species, MOSSCOV expressed in % ground cover.

incorporating phenological aspects of habitat utilization. Directions of captures (table 2) were then analyzed in order to group the capture data in different periods of activity based on

seasonal patterns of movement (i.e. movement away from aquatic overwintering sites in Spring, movement within a summer foraging range, and movement towards aquatic overwintering sites in Fall).

Chi-square values (table 7a) showed significant movement for period 1,2 and 5. Individuals captured in the Fall seem to move back towards the lake where they presumably overwinter. A stepwise regression model associated with this period (model 3) would thus characterize habitat used during Fall migration. Although we got significant chi-square in early season (sampling periods 1 and 2), interpretation is doubtful whether or not there was a migration movement from the overwintering site (i.e. from south and east). To test for an actual movement, we associated the two compass directions in the general direction towards the overwintering site and we tested them against the two compass directions in the general direction away from the overwintering site (i.e. north and west). No significant movement was then noted (table 7b). Consequently, we referred to the phenology of the leopard frog described by Dole (1967) and Rittschof

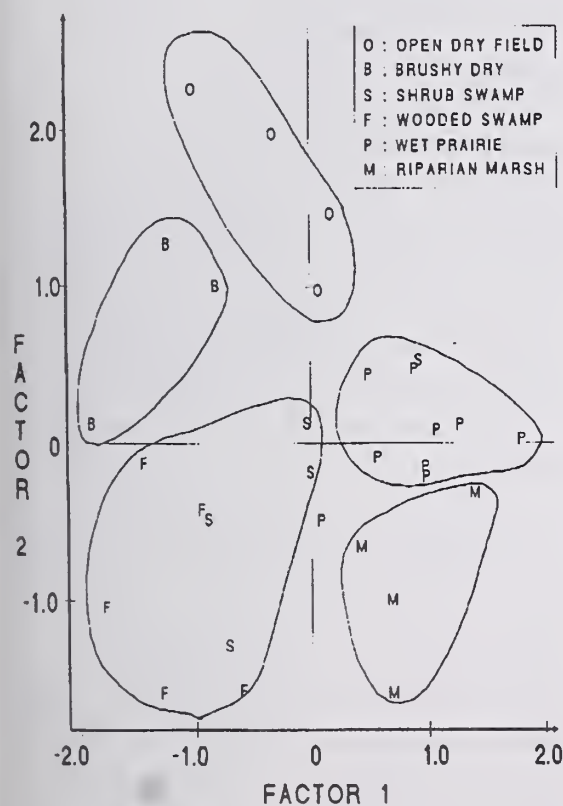


Figure 4a.—Ordination of the sampling stations in the plane defined by the first two principal components according to station physiognomy.

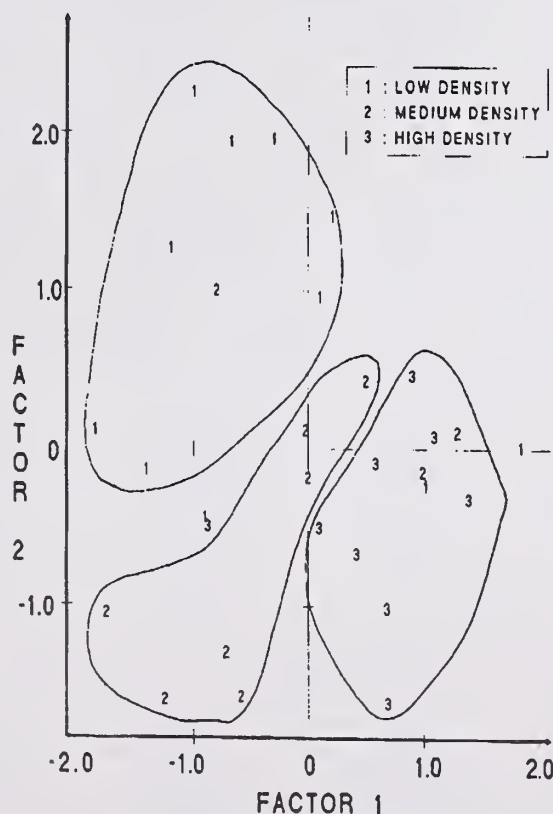


Figure 4b.—Ordination of the sampling stations in the plane defined by the first two principle components according to frog abundance. 1: number of capture < 9; 2: 8 < number of capture < 26; 3: number of capture > 25.

(1975) to decide for grouping of sampling periods.

In May, as leopard frogs remained at proximity of their reproductive site and because we had only 24 sampling stations at that time, data from period 1 were analyzed separately (model 1). Data from June, July and August (periods 2, 3 and 4) were grouped together to construct a single model (model 2) because in June individuals normally tend to disperse in their summer foraging habitats (Rittschof, 1975), and in July and August no definite movement direction was observed (that is typical when foraging habitat is occupied). We also analyzed the data for all periods in two general models (models 4 and 5).

Model 1 (table 8) explains ca. 82% of the variation in frog density for the month of May using 6 variables. The first one is distance to marsh

Table 7a.—Capture data by sampling period and by direction and chi-square values for tests of goodness of fit. P values ≤ 0.05 are considered significant.

Month	North	West	South	East	Exp.value	χ^2	P
May	45	24	24	41	33.50	9.42	<0.025
June	42	28	27	52	37.25	11.56	<0.010
July	26	19	15	25	21.25	3.80	>0.25
August	19	24	31	23	24.25	3.08	>0.25
Sep.-Oct.	106	13	26	33	44.50	117.96	<0.001

Table 7b.—Results of test for nonrandom distribution of captures among the two general directions of movement from and away overwintering sites.

Month	North + West	South + East	χ^2	χ^2_c	P
May	69	65	0.119	0.067	>0.75
June	70	79	0.272	0.215	>0.50
July	45	40	0.294	0.188	>0.50
August	43	54	1.247	1.031	>0.25
Sep.-Oct.	119	59	20.224	19.556	<0.001

χ^2_c = Chi-square with Yates correction for continuity.

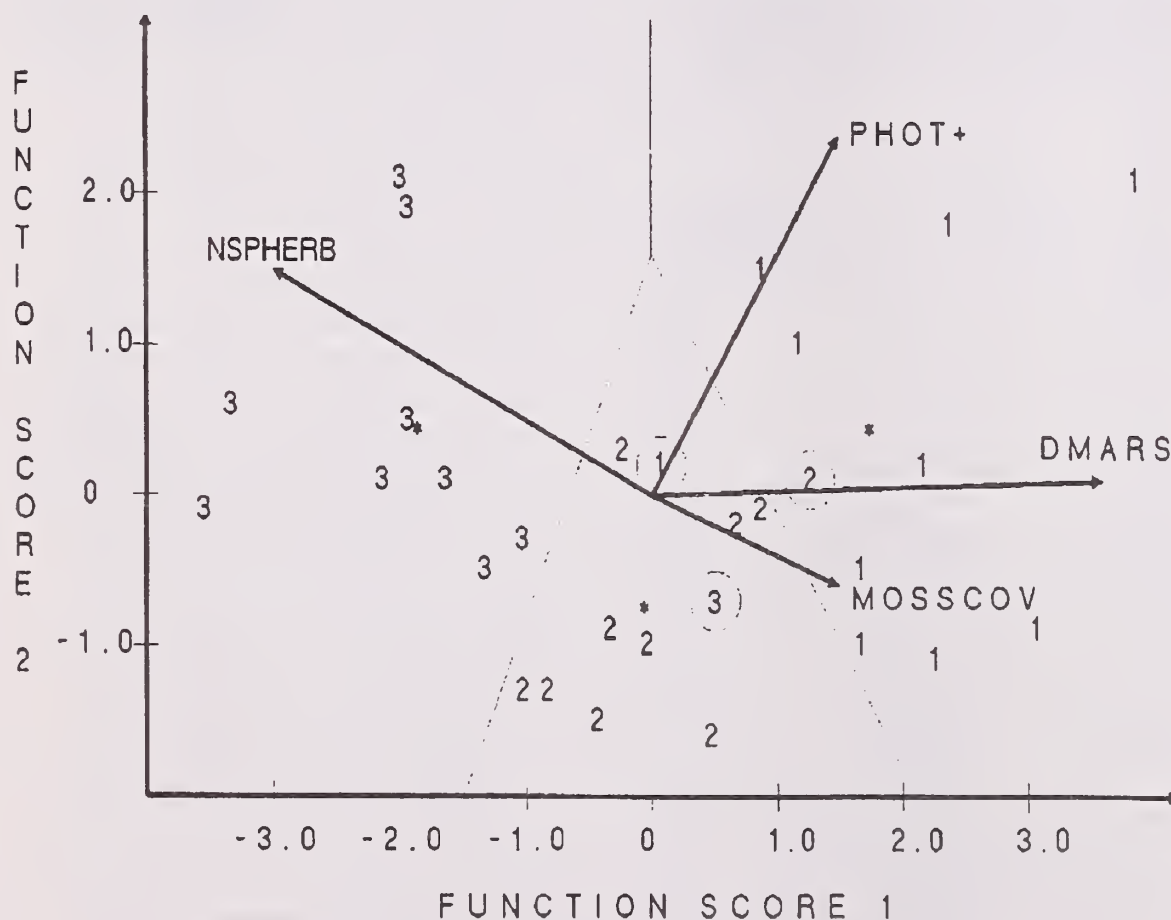


Figure 5.—Localization of the sampling stations (represented by their abundance class) in the discriminant space according to their function score. The relative contribution of each variable (NSPHERB, PHOT+, DMARSH AND MOSSCOV) involved in the two discriminant functions is indicated by the length of each vector. Class centroids are represented by *. Misclassified stations are circled.

line. Four of the five other variables are related to soil characteristics: temperature, moisture, silt fraction and bare ground. In model 2 (summer feeding habitats), about 70% of variation in frog density is explained by only three variables: distance to marsh line, number of herb species and clay fraction. The third model, for the month of September and October, explains only 34.6% of variation in Fall captures with two variables: DMARSH and NSPHERB. It should be noted that the same two variables explain 61.5% of the variation in model 2.

In the next two models (table 8) the seasonal captures were corrected to account for the lower number of stations sampled in May. Model 4 includes five variables: DMARSH and NSPHERB again, and three variables related to vegetation structure (PHOT+, PHOT20, PHOT50). These last three variables explain an additional 21.6% of the variation in frog density in the model.

Flooding of St. Lawrence river over our study sites is a major manifestation in the Lac Saint Pierre area

having a strong impact on frog distribution as indicated by the presence of the variable DMARSH in all previous models. However, when water recesses, we get a mosaic of habitats that can be found elsewhere in North America but independently of the presence of such marsh line. That is the reason why we ran another multiple regression (model 5) after hav-

ing removed DMARSH. This last model emphasizes the significance of vegetation, all 5 variables included being related to vegetation structure. This model explains 69.2% of the variation in total captured frogs.

To facilitate the understanding of our interpretation, we present in appendix 2 the significant level of the Pearson rank correlations between

the variables used in the models (1 to 5 and DFA) and all other variables measured in the field.

Discussion

Model-Related Assumptions

In order to use density (estimated by captures) as the dependent variable in multivariate analysis to model seasonal habitat structure selected by leopard frogs, certain assumptions must be made. Moreover, we cannot recommend the use of the models presented in table 8 to predict density for leopard frog populations for which the pattern of seasonal fluctuation and causes of those fluctuations are unknown (Clawson et al. 1984, Hine et al. 1981).

1. Density as estimated by capture reflects density in the sampled habitats as regards to immigration or emigration to or from neighboring habitats (Collins and Wilbur 1979). *Rana pipiens* is known to be very mobile (Merrell 1977, Rittschof 1975), and is capable of nocturnal excursions of 100 m or more (Dole 1965a). Nevertheless, leopard frogs rarely move more than 10 m away from their home range, estimated by Dole (1965b) to vary between 68 and 503 m².
2. Favorable habitats are characterized by frog densities that are higher than those in unfavorable habitats (Partridge 1978). However, if density is low (as observed on our study site in 1987 when compared to 1986), all favorable habitats may not be occupied (Partridge 1978).
3. Multivariate analyses are based on matrices of linear correlation between environ-

Table 8.—Multiple regression models for frog captures.

Variable	Coefficient ($\beta \pm SE$)		Probability (α value for F)	Adjusted R ²
Model 1 Capture in May (24 stations)				
(Intercept)	-2.51	± 3.60	0.4950	0.4950
DMARSH	-0.0116	± 0.0027	0.0005	0.484
TEMP	0.176	± 0.050	0.0027	0.574
MOIST	0.230	± 0.053	0.0004	0.636
PHOT50	-1.430	± 0.429	0.0039	0.691
SILT	0.284	± 0.074	0.0013	0.770
BAREGRND	-0.999	± 0.419	0.0290	0.818
Model 2 Captures in June, July and August				
(Intercept)	6.05	± 2.99	0.0532	
DMARSH	-0.0355	± 0.0044	0.0000	0.298
NSPHERB	0.649	± 0.153	0.0002	0.615
CLAY	0.151	± 0.051	0.0068	0.700
Model 3 Captures in September and October				
(Intercept)	1.21	± 3.54	0.7358	
DMARSH	-0.0196	± 0.0056	0.0016	0.121
NSPHERB	0.663	± 0.204	0.0030	0.346
Model 4 Adjusted total captures				
(Intercept)	-6.80	± 8.03	0.4053	
DMARSH	-0.0600	± 0.0099	0.0000	0.351
NSPHERB	1.745	± 0.362	0.0001	0.553
PHOT+	-14.859	± 3.001	0.0000	0.607
PHOT20	4.100	± 1.274	0.0037	0.693
PHOT50	4.804	± 1.576	0.0055	0.769
Model 5 Adjusted total captures*				
(Intercept)	17.64	± 11.37	0.1339	
HGH	20.307	± 2.732	0.0000	0.196
LITTHICK	-6.275	± 1.264	0.0000	0.362
PHOT+	-14.060	± 3.081	0.0001	0.450
PHOTCAN	-5.234	± 1.374	0.0009	0.631
MBLH	5.195	± 2.135	0.0228	0.692

*DMARSH removed from the model 4.

mental variables and an index of abundance (Legendre and Legendre 1984), which neglects saturation and negative feedback effects, as well as non-linear patterns in the species response to environmental factors.

4. Competition and predation or the presence of sites for reproduction may control frog distribution patterns but

active habitat selection with respect to vegetation structure also plays an important role. Dole (1971) has observed that newly metamorphosed young do not necessarily select the first suitable site during dispersal.

Finally, in models, it is apparently essential to assume that factors vital for species survival, i.e. those variables actively selected by individu-

als, and those identified by the analysis do not necessarily coincide. In fact, apparent cause-and-effect relationships are not often testable and require specific study on the functional responses of species to the selected variables. Weller (1978) indicates that the study of habitat stimuli as attractants for wildlife remains to be done. The approach used in this study is valuable when variables describing favorable habitat are required (Clark and Euler 1982, Green 1971, Grier 1984).

Classification of Habitats

The PCA analysis facilitated understanding of the multidimensional models, and so allowed for systematic description of the various habitats found in the Lac Saint Pierre floodplain. We found that our pre-established groupings were not an analytical artefact but rather confirms that there is a structure that can be defined by environmental variables not related to species specific local vegetation.

Our results have shown that different age groups of *R. pipiens* are not differently distributed among habitats (tables 3 and 4). This conclusion have been drawn with recently metamorphosed young representing only 16% of total captures but is supported by others studies describing the habitats used by young (Dole 1971, Hine et al. 1981, Rittschof 1975, Whitaker 1961). Our proposed models are those independent of age or size groups. This might not be the same however, for other species as Clark and Euler (1982) and Roberts and Lewin (1979) have noted for *Rana clamitans* and for *R. sylvatica*, respectively.

The models presented in this paper reveal the importance of distance to marsh line in habitat classification. This variable has a high degree of predictive power as to the extent habitat will be utilized by leopard frogs, in the Lac Saint Pierre

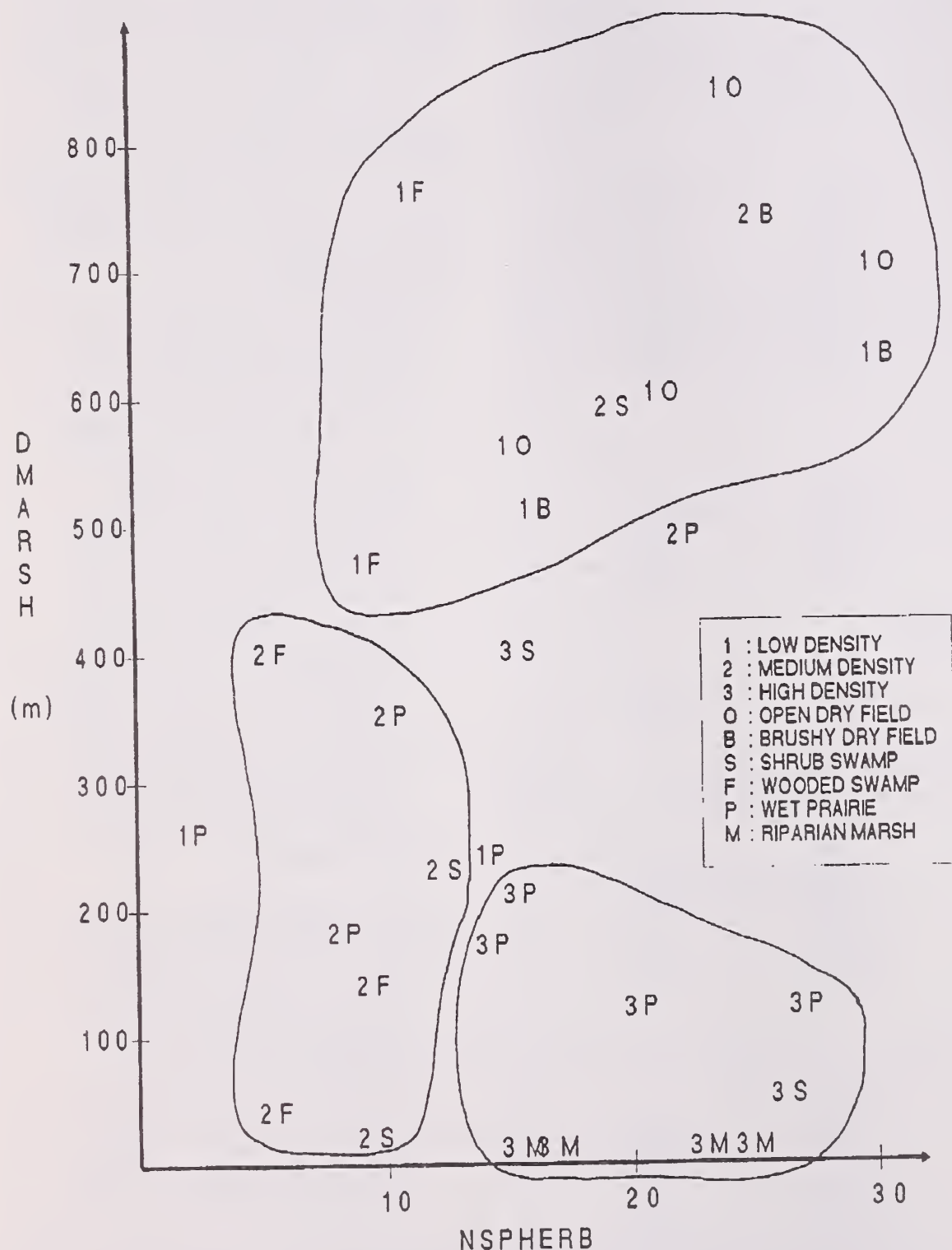


Figure 6.—Ordination of the stations in relation to marsh distance (DMARSH) and number of herb species (NSPHERB). Stations with the same abundance class are circled by an ellipsoid.

floodplain. However, systematic sampling in habitats of unknown value indicates the presence of a significant number of leopard frogs in some wooded and shrub swamps stations far from the marsh (fig. 6). The DFA model is then relevant to show the importance of variables related to structural components of habitat such as herbaceous vegetation (PHOT+, NSPHERB) and moss cover (MOSSCOV). In a similar analysis on Missouri herpetofauna, Clawson et al. (1984) concluded that proximity to water appeared to override other variables in determining the abundance of amphibians.

Other multivariate studies (Beebee 1977, Clark and Euler 1982, Dale et al. 1985 and Gascon and Planas 1986) on anuran species habitat have shown that bio-physico-chemical variables related only to the body of water cannot give predictive information about the absence or presence of a respective amphibian species.

Frog Abundance Models

In spring, before the growing season, frog distribution is related to soil characteristics, such as temperature. This variable is not significantly correlated with any other variable measured. It results from the interaction of many variables and may be a key element in habitat selection during that period. The activity of ectotherms is known to be related to ambient temperatures (Putnam and Bennett 1981), by selecting warmer habitat, ectotherms might improve their mobility, thus escaping more easily to predators. Soil moisture is the third most important variable in the first model and appears only in this model. In spring, soil moisture reflects the speed of water recess after snowmelt and obviously is a variable linked with the proximity of overwintering and spawning sites.

The model proposed for the summer period is the simplest of the models presented in this paper with

only 3 descriptors (DMARSH, NSPHERB, CLAY). Soil moisture is not included into this model although it has been shown to be the major factor limiting the distribution of anuran species in terrestrial habitats (Clark and Euler 1982, Dole 1965a, 1971, Rittschof 1975, Roberts and Lewin 1979). It may be that this variable contains an information already carried in DMARSH variable; its presence in the summer model would then be a redundancy. Clay, on the other hand, is a variable known to play an important role in soil water retention (Ramade 1984).

Sampling during Fall migration have shown a significant movement towards aquatic overwintering sites. Model 3 however, with two variables explaining only 34.6 % of frog abundance, did not allow identification of preferred migratory corridors. It seems that leopard frogs en route to overwintering sites do not select any particular pathway.

The last two models use data from all sampling periods. Model 4, which improves on model 2 (summer model), is interesting because its photometric variables are significantly correlated (appendix 2) with many of other variables describing the habitat structure. This suggests the value of such indices (Fox 1979) in habitat modeling to quantify vegetation structure since they can be measured with an instrument (light meter) easy to use.

The last model, with 69.2% variability explained, is of more general interest because the local variable DMARSH has been removed. In model 5, the importance of vegetation structure in habitat selection is obvious, and the model can be applied to the entire distributional range of *R. pipiens*. HGH indicates the importance of graminoids (grasses, sedges, etc.) usually abundant in open wetlands. This vegetation cover provides a refuge from many predators and may thus contribute to maintaining an abundant frog population (Whitaker 1961). Lit-

ter thickness has a negative coefficient in the model, but is positively correlated with HGH, which suggests the existence of an optimum foliage density. Dole (1965b, 1967, 1971) mentions that litter may preclude direct contact between the individual and the moist substrate and thus cause higher cutaneous evaporation. The three other descriptors summarize the information on vegetation structure. PHOT+ corresponds to the presence of broad-leaf herbs > 100 cm tall ($R_p = .4066$, $P = 0.026$), and graminoids ($R_p = .3765$, $P = 0.040$); PHOTCAN represents tree and shrub cover; MBLH indicates broad-leaf plant obstruction between 20 and 100 cm from the ground.

These results seem to indicate that vegetation structure, more than specific species composition, is an important factor in habitat selection for *Rana pipiens*. This finding is similar to that of MacArthur and MacArthur (1961) who have demonstrated that bird species occupying forests and prairies choose their habitat on the basis of foliage density at different levels from the ground, irrespective of plant species composition.

Conclusion

In summary, we present three types of complementary analysis dealing with wet habitats used by the leopard frog during Summer. First, a PCA gives a qualitative description of five kinds of habitats typical to the St. Lawrence river floodplain and offering potential supports to leopard frog populations. Second, a DFA model with four easily measured variables allows classification of habitats into three groups of frog abundance. This is a very helpful way to map potential frog species habitats for protective purpose. Finally, five regression models (according to each phenological periods or whole active season) explain frog abundance variations with only a few important structural variables.

Although the models described in this paper cannot fully demonstrate functional relationships between model variables and frog density, suitable modifications of some of these variables (litter thickness, for instance) may increase frog population. Refinement of these models will require experimental studies on functional responses of leopard frogs to specific habitat features.

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Appendix 1.

Abbreviations for variables used in the text, figures and tables.

Abbreviations	Variables	Abbreviations	Variables	Abbreviations	Variables
DOPEN	Distance to nearest open habitat	BASAREA	Basal area	PHOT100*	Photometric index, between 50 et 100 cm
DCLOSE	Distance to nearest closed habitat	MINAREA _N	Minimal area	PHOT+*	Photometric index, for herbs > 100 cm
DMARSH	Distance to marsh line	PH	pH of soil solution	PHOTCAN*	Photometric index under shrub and tree strata
DWATERP	Distance to nearest permanent pool	SAND	Sand fraction in soil	HERBHIGHT*	Height of herb stratum
DHUMAIN	Distance to nearest human artefact	SILT	Silt fraction in soil	HERBCOV*	% herb cover
ALTREL	Altitude relative to shore line	CLAY	Clay fraction in soil	HGH*	Cover class for high graminoid herbs (> 100 cm tall)
NSPHERB	Number of herbaceous species	DWATER*	Distance to nearest temporary pool	HBLH*	Cover class for high broad-leaf herbs
NSPSHRUB	Number of shrub species	MOIST*	% soil moisture	MGH _N *	Cover class for medium graminoid herbs (20 to 100 cm)
NSPTREE	Number of tree species	TEMP*	Temperature at the soil surface	MBLH*	Cover class for medium broad-leaf herbs
TREE	Cover class for tree stratum	WTABLE*	% bare ground	SMALLH*	Cover class for herbs < 20 cm tall
SHRUBHI	Cover class for High shrub stratum	BAREGRND _N *	Water table level		
SHRUBLO	Cover class for low shrub stratum	LITTER*	% ground covered with litter		
		MOSSCOV _N *	% moss cover		
		DEADWOOD*	% ground covered by dead wood		
		LITTHICK*	Litter thickness		
		PHOT20*	Photometric index, between 0 and 20 cm		
		PHOT50*	Photometric index, between 20 and 50 cm		

N: Variable normalized by square-root transformation.

**: Variable measured monthly.*

Appendix 2.

Significance levels of Pearson rank correlations between the variables included in the models and all variables measured. (Significance levels 1: $P \leq 0.05$; 2: $P \leq 0.01$; 3: $P \leq 0.001$; 4: $P \leq 0.0001$; +: positive; -: negative.)

Models	1						2		4			5				D
	D M A R S H	T E M P S	M O I S T	P H O T 5 0	S I L T G R N D	B A R E N D	N S P H E R B	C L A Y	P H O T +	P H O T 2 0	P H O T 5 0	H E R B H I G H T	L I T T H I C K	P H O T C A N	M O I S T H E R B C O V	M O I S T H E R B C O V
DOPEN									-1		-1	-2	-1	+1	+1	
DCLOSE									+1							
DMARSH			-1									-1				
DHUMAN																
ALTREL	+3		-1				+1									
NSPHERB																
NSPSHRUB	+3		-1							-1		-1	-1	+1		+3
NSPTREE					+2		-1		-1	-2	-1	-3	-1	+1	+2	+2
BASAREA					+2		-2			-2		-3	-2	+1	+2	+1
MINAREA			-1										-3	+2		+2
PH																
SAND				-2				-4							-1	
SILT															-2	
CLAY																
BAREGRND													-2		+1	+1
LITTER					-2				+1	+1			+2			-2
MOSSCOV		-1										-2	-1			
DEADWOOD							-1						-1	+1		
LITTHICK					-4					+2		+3		-2	-2	-3
TREE					+1		-1		-1	-1		-3	-2	+2	+2	
SHRUBHI									-2	-1		-1	-2	+3		+1
SHRUBLO									-1				-1	+2		+2
MOIST	-1											+1		-1		-1
TEMP																
PHOT20									+1		+1	+2	+2	-1		
PHOT50									+2	+1		+2		-1		
PHOT100	-1						-1					+1				-2
PHOT+										+1	+2	+1		-2		
PHOTCAN			-1						-2	-1	-1		-2			+1
HERBHIGHT											+1	+3	+1			-2
WTABLE			+3													
D.WATER																
HERBCOV										+1				-2		-2
HGH	-1								+1	+2	+2		+3	-1	-2	-2
HBLH							-1		+1		+1					
MGH	+2															
MBLH												-1	-2			
SMALLH												-2	-2			

D: DFA model.

Habitat Correlates of Distribution of the California Red-Legged Frog (*Rana aurora draytonii*) and the Foothill Yellow-Legged Frog (*Rana boylei*): Implications for Management¹

Marc P. Hayes and Mark R. Jennings²

The application of habitat analysis to management has a long, complex history. The Greek philosopher Aristotle inferred that seasonal variation in the distribution of certain commercially exploited fishes was related to changes in their food resources and habitat temperatures (Cresswell 1862). In the 13th century, the Mongol emperor Kublai Khan encouraged the gathering of data on foraging patterns of sport-hunted birds to facilitate manipulating their populations (Leopold 1931). Since these efforts, many individuals have used diverse habitat data to help understand factors that influence the distribution and success of various species. Most often, such data have been used to address commercially important or game species, usually to identify management alternatives intended to enhance existing populations or avert population declines (Bailey 1984, Leopold 1933). This emphasis has resulted in most studies addressing selected birds,

fishes, and large mammals. In contrast, species historically having limited economic importance (i.e., "non-game" species) have been largely neglected (Bury 1975; Bury et al. 1980a, b; Pister 1976). Only over the last 15 years has an appreciation been broadly realized that non-game species are also in need of management. Non-game species are often linked to economically important ones, and as such, provide significant direct and indirect benefits to humans (Kellert 1985, Neill 1974). Although this appreciation has led to greater emphasis in their study (Bury et al. 1980a, Pister 1976), a broader understanding of the biology of non-game species is increasingly urgent because of widespread habitat modification influencing declines among ever-greater numbers of such species (Dodd 1978, Hayes and Jennings 1986, Hine et al. 1981, Honegger 1981).

Amphibians are prominent among groups of organisms given a non-game label (Bury et al. 1980a). For ranid frogs, among the most familiar of amphibian groups, non-game is really a misnomer (Brocke 1979) because they have a history of human exploitation which has its roots in European and aboriginal cultural traditions (Honegger 1981, Zahl 1967) and has included significant commercial enterprises (Abdulali 1985, Chamberlain 1898, Husain and Rahman 1978, Jennings and Hayes 1985,

Abstract.—We examined features of the habitat for the California red-legged frog and foothill yellow-legged frog from the Central Valley of California. Limited overlap exists in habitat use between each frog species and introduced aquatic macrofaunal predators. Temporal data implicate aquatic predators that restrict red-legged frogs to intermittent stream habitats as explaining limited overlap. Identification of responsible predators is currently prevented because the alternative of limited overlap simply due to differential habitat use between frogs and any one putative predator cannot be rejected. Until the predators causing the negative effects are identified, efforts should be made to isolate these frogs from likely predators and minimize alteration of key features in frog habitat.

Wright 1920). Despite this history of exploitation, few attempts have been made to link species-specific habitat requirements of ranid frogs to their management (but see McAuliffe 1978; Treanor 1975a, b; Treanor and Nicola 1972). Most "management" literature has either simply reviewed the biology of selected ranid frog species or indicated vulnerable life history stages needing study (Baker 1942, Bury and Whelan 1984, Storer 1933, Willis et al. 1956, Wright 1920).

In this report, we examine the habitat features of two "non-game" species, the California red-legged frog (*Rana aurora draytonii*) and the foothill yellow-legged frog (*Rana boylei*), two ranid frogs found in lowland California. Each species has disappeared from sizable areas of its historic range (Hayes and Jennings 1986, Sweet 1983). Although historical disappearance of red-legged frogs has been linked to its exploitation as food (Jennings and Hayes 1985), causal factors in the continuing decline of both species remain poorly understood. Insufficient documentation of the habitat requirements of each species has especially impeded identification of the causes of decline (Hayes and Jennings 1986). In this report, we reduce this gap by identifying the habitat requirements that characterize each frog. We then use these data to suggest the direction for management of these two species

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until experiments can identify the causes of decline.

METHODS

Our analysis draws upon two data sets, one addressing *R. a. draytonii* and the other, *R. boylei*. The former is based on all known occurrences of *R. a. draytonii* (n = 143) from the Central Valley of California, which we define as the collective drainage area of the Kaweah, Kern, Sacramento-San Joaquin (to Carquinez Strait), and Tule River systems. We assembled these data from museum records and

field notes or direct observations of the many investigators listed in the acknowledgments or whose data are cited in Childs and Howard (1955), Cowan (1979), Fitch (1949), Grinnell and Storer (1924), Grinnell et al. (1930), Hallowell (1854, 1859), Ingles (1932a, b; 1933; 1936), Storer (1925), Walker (1946), Williamson (1855), and Wright and Wright (1949). We used records not authenticated by museum specimens if they were corroborated by at least two sources. We then determined the subset (n = 131) of records that could be both mapped (i.e., where we could identify the aquatic system likely to be

the site of origin of the source population upon which the record was based), and identified as being from different "point" localities (≥ 0.4 km apart). Although our data set was developed primarily from this subset, we used a few data from the remaining 12 localities for the habitat variables described below. We used this additional data because they were either available with the original records or could be determined independent of accurate mapping.

For each locality, we recorded as many of 12 habitat variables as possible (table 1). For aquatic habitat type, we used the term "stream" for localities with both a well-defined drainage inflow and outflow, whereas we used "pond" for localities lacking a well-defined inflow and little or no outflow. Temporal status of the aquatic habitat was scored as perennial or intermittent based on 7.5' and 15' United States Geological Survey (USGS) topographic maps, but the status of some localities was modified based on field reconnaissance or data provided by other investigators. For many localities, lack of change in the temporal status of the aquatic habitat during the time *R. a. draytonii* was recorded was verified by examining USGS topographic maps bracketing the frog record date(s). We used the designation intermittent to describe the interruption of surface flow in streams or complete dry-down in ponds, either occurring at least once seasonally. Drainage area indicates the size of the hydrographic basin influencing the recorded locality. The drainage area, local gradient, and stream order were largely estimated from 7.5' USGS topographic maps. We estimated large drainage areas (>130 km²) by extrapolation to the recorded locality on topographic maps from either the drainage area for the nearest upstream gauging station (United States Geological Survey 1970a, b) or section counts on United States Forest Service and county maps. Local gradient was estimated from map

Table 1.—Habitat variables recorded for the California red-legged frog (*Rana aurora draytonii*) data set. Subset scored refers to the subset of localities for which we were able to score each variable. Percent scored refers to the percentage of the entire data set (n = 143) for which we were able to score each variable. See text regarding further details concerning the method of data collection for each variable.

	Variable	Subset scored (n =)	% scored	Definition
1.	Habitat type	140	98	As (1) stream or (2) pond
2.	Temporal status	137	96	As (1) perennial or (2) intermittent
3.	Drainage area	129	90	In km ²
4.	Local gradient	139	97	In angular degrees (°) from horizontal
5.	Water depth	74	52	As (1) presence or (2) absence of water ≥ 0.7 m deep
6.	Vegetation matrix (emergent or shoreline)	44	31	As (1) dense (area $\geq 25\%$ thickly vegetated) (2) limited (some, but <25% of area) (3) absent
7.	Native fishes	56	39	As (1) present or (2) absent
8.	Introduced fishes	32	22	As (1) present or (2) absent
9.	Introduced bullfrogs	115	80	As (1) present or (2) absent
10.	Substrate alteration	113	79	As (1) present or (2) absent
11.	Vegetation reduction	106	74	As (1) present or (2) absent
12.	Stream order	127	89	As defined by Strahler (1957)

distances of 0.5-1.0 km across the recorded locality except in the few cases where pronounced local relief required reduction of this distance for an accurate estimate.

Data for the remaining variables (water depth, vegetation matrix, native and introduced fishes, introduced bullfrogs [*Rana catesbeiana*], substrate alteration, and vegetation reduction) were obtained for subsets of the larger data set from the sources indicated earlier supplemented by Leidy (1984), Moyle and Nichols (1973), Moyle et al. (1982), and Rutter (1908). The exact values used to partition water depth and vegetation matrix variables are arbitrary. However, we chose their general dimensions with the intent of identifying whether the habitat requirements of red-legged frogs suggested by anecdotal data (moderately deep water associated with dense vegetation; see Hayes and Jennings 1986) were supported by this data set. Variation in the collective data set required scoring the fish and introduced bullfrog data as presence/absence, but we also used available data on which fish species were present to interpret the habitat requirements of red-legged frogs. Substrate alteration and vegetation reduction variables indicate alteration of aquatic habitats that was, directly or indirectly, human-effected. We scored substrate alteration as present if evidence existed that the shoreline or substrate topography of the aquatic habitat had been markedly altered (e.g., dams, rip-rap, bank-trampling by cattle). Marked alteration meant that at least 25% of the area of substrate of a locality appeared altered. We scored vegetation as being reduced when data indicated that at least 25% of pre-existing shoreline or emergent vegetation had been removed.

We also gathered current data on a subset of the described localities through field reconnaissance and some information provided by others (data gathered during the interval

1980-1987 represented "current" data). We used these data to help identify temporal changes that may have occurred at sites or in drainage systems for which we had historical data. For this analysis, we used "drainage system" to mean only the primary and highest-order (*fide* Strahler 1957) secondary tributaries of the Sacramento-San Joaquin drainage system. These data were particularly important for indicating where red-legged frogs were probably extinct.

The data set addressing *R. boylei* consists of data published by Moyle (1973) and Moyle and Nichols (1973) from which we re-examined selected elements. Collection methods for these data are thoroughly described therein. Our reanalysis used most of the variables described by Moyle (1973) with some modifications. We used the original estimates of the numbers of each fish species rather than the coded values; the numbers of yellow-legged frogs and bullfrogs remained coded because the original data were recorded as coded. Moyle's stream type variable was reduced to two categories by combining his three intermittent and three perennial stream categories. We also added two variables, one which combines Moyle's cobble and boulder/bedrock substrate categories. The other describes the stream morphology category designated in Moyle's original data as smooth water and fits the definition of a run (Armour et al. 1983). For correlations between yellow-legged frogs and other species, we used only the subset of localities where either or both of yellow-legged frogs and the species being compared was present.

We re-examined these data for four reasons. First, Moyle (1973) summarized data from only some of the sites where yellow-legged frogs were not found. We were equally interested in habitat variation among all sites sampled where yellow-legged frogs had not been found as well as sites where they were found.

Second, Moyle (1973) found that the collective abundance of all fish species was inversely correlated with that of yellow-legged frogs, but also commented that yellow-legged frogs were most abundant where native fishes were present. Because original estimates of the numbers of each fish species were available and an inverse relationship between the abundance of native frogs and introduced fishes had already been identified (Hayes and Jennings 1986), we were especially interested in relationships between the abundance of specific native and introduced fishes and that of yellow-legged frogs. Third, Moyle (1973) coded fish abundance when the data, as originally recorded, permit at least ranking, so, where possible, we analyzed the original data directly to minimize bias that can result from coding (Sokal and Rohlf 1981). Lastly, the fish abundance data displayed skewed distributions for several species, so we used non-parametric analyses to avoid having to make any assumptions about sample distributions.

Statistical treatments used are described in Sokal and Rohlf (1981) and Zar (1974). All contingency table comparisons performed had one degree of freedom (df), so all Chi-square values were calculated with the correction for continuity (X^2_c). For those analyses that required more than one comparison using some of the data, alpha (α) was evaluated based on the number of comparisons to a level equivalent to 0.05 using Sidak's multiplicative inequality (Sokal and Rohlf 1981).

RESULTS

California Red-Legged Frog

Rana aurora draytonii was recorded primarily from aquatic habitats that were intermittent streams which included some area with water at least 0.7 meters deep, had a largely intact emergent or shoreline vegetation,

and lacked introduced bullfrogs (table 2). We found descriptions adequate to characterize vegetation for 77% (33) of sites where the emergent or shoreline vegetation variable could be scored. With three exceptions, descriptions indicated that either, or both of, an emergent vegetation of cattails (*Typha* spp.) or tules (*Scirpus* spp.), or a shoreline vegetation of willows (*Salix* spp.) were present. Shrubby willows were recorded at 67% (22) of the sites with vegetative descriptions, and were identified as arroyo willow (*Salix lasiolepis*) in the eight instances where a species name was provided. Only juvenile frogs were recorded at five of the six sites where a limited emergent vegetation was present and at the only site that lacked a water depth greater than 0.7 m. We found no significant difference in the numbers of intermittent versus perennial

sites with red-legged frogs that had a dense vegetation and a water depth of ≥ 0.7 m ($X^2_c = 0.338$, $p = 0.561$, for

vegetation; $X^2_c = 0.017$, $p = 0.897$, for water depth; $X^2_{df=1, \alpha=0.025} = 5.024$ for both).

Rana aurora draytonii was also more frequently recorded at sites with native fishes and with substrate alteration, but less frequently recorded at sites with introduced fishes. Fishes were present at 69% (40 of 58) of sites where data as to their occurrence were recorded; 26 sites had only native fishes, seven had only introduced fishes, and seven had both. Only four fish species, California roach (*Lavinia symmetricus*), hitch (*Lavinia exilicauda*), green sunfish (*Lepomis cyanellus*), and mosquitofish (*Gambusia affinis*), were recorded as co-occurring with *R. a. draytonii* at more than three sites (table 3), and only California roach was recorded at more than 25% (10) of sites. Sixty of the 70 sites described as being substrate-altered at the time *R. a. draytonii* was recorded were small impoundments.

California red-legged frogs were also most frequently recorded at sites influenced by a small drainage area, having a low local gradient, and in streams having a low stream order. Drainage areas of sites from which *R. a. draytonii* was recorded vary from 0.02 km² to over 9000 km², but two-

Table 3.—Frequency of fish species co-occurrence with *Rana aurora draytonii*. Percentage is the number of sites respective fish species were recorded as a function of all sites where fishes were recorded as co-occurring with *R. a. draytonii*. An asterisk (*) indicates introduced species.

Species	Co-occurrence Percentage	
	(n =)	(%)
California roach (<i>Lavinia symmetricus</i>)	19	47
Mosquitofish (<i>Gambusia affinis</i>)*	10	25
Hitch (<i>Lavinia exilicauda</i>)	6	15
Green sunfish (<i>Lepomis cyanellus</i>)*	6	15
Threespine stickleback (<i>Gasterosteus aculeatus</i>)	3	8
Sacramento squawfish (<i>Ptychocheilus grandis</i>)	2	5
Sacramento sucker (<i>Catostomus occidentalis</i>)	2	5
Prickly sculpin (<i>Cottus asper</i>)	1	3
Hardhead (<i>Mylopharodon conocephalus</i>)	1	3
Rainbow trout (<i>Salmo gairdnerii</i>)	1	3
Brown trout (<i>Salmo trutta</i>)*	1	3

Table 2.—Variation among habitat variables for California red-legged frogs (*Rana aurora draytonii*). Number of localities (percentages of localities) in each category are indicated. See table 1 and text for explanation of variable categories.

Variable		Variable categories	
1.	Aquatic habitat type	(a) stream	129 (92%)
		(b) pond	10 (8%)
2.	Temporal status of aquatic site	(a) perennial	49 (36%)
		(b) intermittent	88 (64%)
3.	Water depth	(a) ≥ 0.7 meters	73 (99%)
		(b) < 0.7 meters	1 (1%)
4.	Emergent and shoreline vegetation	(a) absent	0 (0%)
		(b) limited	9 (20%)
		(c) dense	35 (80%)
5.	Native fishes	(a) present	33 (65%)
		(b) absent	18 (35%)
6.	Introduced fishes	(a) present	14 (44%)
		(b) absent	18 (56%)
7.	Introduced bullfrogs	(a) present	13 (11%)
		(b) absent	102 (89%)
8.	Significant substrate alteration	(a) present	70 (62%)
		(b) absent	43 (38%)
9.	Significant removal vegetation (see #4)	(a) present	1 (2%)
		(b) absent	44 (98%)
10.	Current status (among localities)	(a) probably extant	86 (72%)
		(b) probably extinct	34 (28%)
11.	Current status (among drainages)	(a) probably extant	18 (42%)
		(b) probably extinct	25 (58%)

thirds (n = 83) are from localities with drainage areas ≤ 40 km² (fig. 1). Local gradient (slope) at California red-legged frog localities varies from 0.04° to 12.8° from horizontal, although 87% (n = 100) occur at sites with slopes $\leq 2^\circ$. California red-legged frogs have been recorded in 1st to 6th order streams, but 94% (n = 119) of these localities are 4th- or lesser-order streams and 42% are 1st-order streams (fig. 2).

Based on the subset for which current data were available (n = 120), California red-legged frogs are probably extinct at >25% of the localities where they were historically recorded. When clustered into a sample representing drainage systems (n = 43; see methods), this subset indicates that California red-legged frogs are probably extinct in over 50% of the drainage systems in the Central Valley area. Three habitat variables (temporal status of aquatic habitat, drainage area, and introduced bullfrogs) showed a significant relationship to the probability of survival of local populations of California red-legged frogs (table 4). We found that *R. a. draytonii* is likely extant at 82% (n = 70) of localities with an intermittent aquatic habitat, whereas it is probably extinct at 71% (n = 22) of the sites with a perennial aquatic habitat. Grouping localities based on drainage area, *R. a. draytonii* is probably extant at 83% (n =

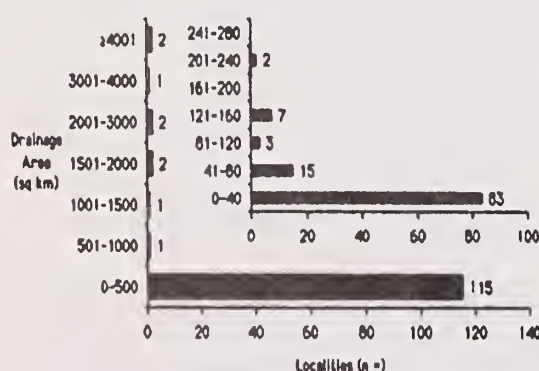


Figure 1.—Frequency distribution of localities where *Rana aurora draytonii* has been recorded in the Central Valley, California based on drainage area. The inset details the frequency distribution of localities with drainage areas < 280 km².

85) of sites influenced by a small (<300 km²) drainage area, whereas it is probably extinct at all recorded localities (n = 11) influenced by a large (≥ 300 km²) drainage area. Moreover, available data indicate that *R. a. draytonii* is extinct at all recorded localities on the Central Valley floor, which includes all localities

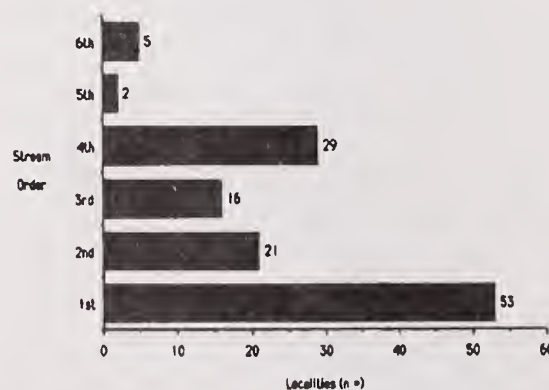


Figure 2.—Frequency distribution of localities where *Rana aurora draytonii* has been recorded in the Central Valley, California based on stream order.

Table 4.—Contingency analysis relating selected habitat variables to an estimate of the likelihood that historically recorded California red-legged frog populations are extant. Status of frog populations at recorded localities are indicated as extant (= probably extant) and extinct (= probably extinct). A double asterisk (**) denotes significant contingency tables, based a critical $X^2_{df=1, \alpha(2)=0.007} = 7.3$, α adjusted for seven comparisons (see methods).

Variable	Condition	Locality Status		X^2_c	Probability
		extant	extinct		
1. Temporal status	Perennial	9	22	27.326	0.0001**
	Intermittent	70	15		
2. Drainage area	≥ 300 km ²	0	11	31.466	0.0001**
	<300 km ²	85	18		
3. Native fishes	+	13	6	0.276	0.5991
	-	14	11		
4. Introduced bullfrogs	+	0	10	27.140	0.0001**
	-	70	16		
5. Substrate alteration ^a	+	25	14	0.983	0.3215
	-	47	14		
6. Introduced fishes	+	5	9	0.003	0.9524
	-	7	10		
7. Substrate alteration ^b	+	21	3	<0.001	0.9944
	-	26	5		

^aAnalysis with all localities.

^bAnalysis with subset of localities having a drainage area ≤ 25 km².

affected by the largest drainage areas (n = 10). Similarly, *R. a. draytonii* is probably extant at 81% (n = 70) of localities lacking introduced bullfrogs and is probably extinct at all localities (n = 10) where it has been recorded with bullfrogs. Remaining variables either failed to show a significant relationship to the probability of California red-legged frog survival (table 4), or one of the variable categories was so rare that this analysis was not applicable (see table 2).

Foothill Yellow-Legged Frog

Rana boylei was recorded primarily from shallow, partly shaded stream sites with riffles and at least a cobble-sized substrate. All 29 stream sites at which either post-metamorphic or larval *R. boylei* were recorded were ≤ 0.6 m in average water depth (fig. 3) and had at least some shading (fig. 4). *Rana boylei* was recorded more

frequently at sites with a stream area that was >20% shaded than at sites with $\geq 20\%$ shading. Only one of 29 *R. boylei* sites lacked riffle habitat and *R. boylei* was recorded significantly more frequently at sites with >40% riffle area than at sites with a riffle area of $\leq 40\%$ [$X^2_c = 8.680$, $p = 0.003$, $X^2_{df=1, \alpha(2)=0.025} = 5.024$; fig. 5]. Only four of 29 *R. boylei* sites lacked at least a cobble-sized substrate and *R. boylei* was recorded most frequently (20 of 29) at sites with >40% of the substrate that was at least cobble-sized (fig. 6). Few other patterns could be identified from among the environmental variables that we re-analyzed. *Rana boylei* was recorded more frequently from perennial streams ($n = 19$) than from intermittent ones ($n = 10$), but the difference was not significant when compared to the total number of perennial ($n = 71$) and intermittent ($n = 59$) stream sites sampled [$X^2_c = 1.268$, $p = 0.260$, $X^2_{df=1, \alpha(2)=0.025} = 5.024$]. Of 13 environmental variables that we re-examined, only the percentage of stream area in riffles was significantly correlated with the abundance of *R. boylei* (table 5).

Rana boylei occurred with 1-5 ($\bar{x} = 2.5$) of the vertebrate members of the aquatic macrofauna at 26 of the 29 localities where it was recorded.

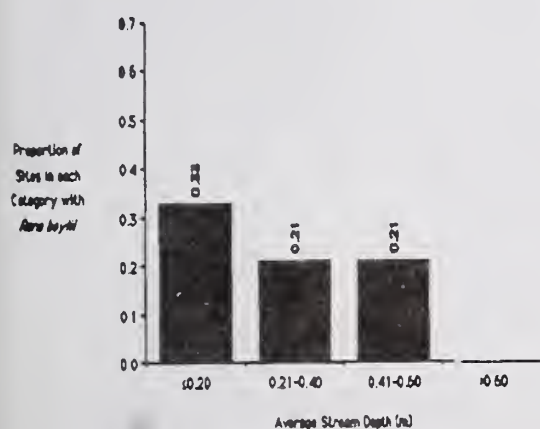


Figure 3.—Histogram of the proportion of sites in stream depth categories where *Rana boylei* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each stream depth category are: <0.20 ($n=8/24$), 0.21-0.40 ($n=9/43$), 0.41-0.60 ($n=12/57$), and >0.60 ($n=0/18$).

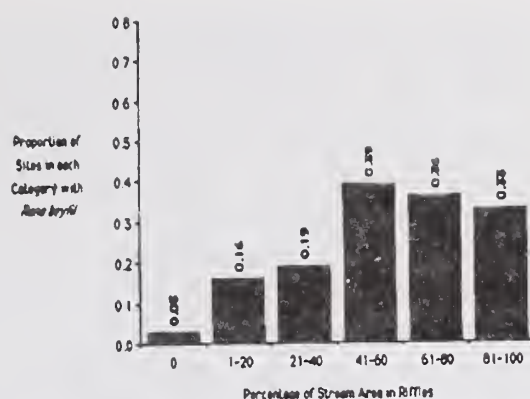


Figure 5.—Histogram of the proportion of sites in riffle categories where *Rana boylei* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each riffle category are: 0% ($n=1/36$), 1-20% ($n=5/31$), 21-40% ($n=4/21$), 41-60% ($n=11/28$), 61-80% ($n=7/19$), and 81-100% ($n=2/6$).

Foothill yellow-legged frogs were recorded as occurring with 12 different species, but co-occurrence, expressed as the percentage of total sites at which either *R. boylei* or the co-occurring species were recorded, did not exceed 31% (table 6). Introduced species ($n = 6$) occurred with *R. boylei* less frequently ($\bar{x} = 2$, 1-3) than native species ($\bar{x} = 9.3$, 1-17) and native species had a significantly higher percentage of co-occurrence (3-31%, $\bar{x} = 16.5\%$) than introduced species [$n = 6$; 2-9%, $\bar{x} = 3.7\%$; Mann-Whitney test, $U' = 32.5$, $p = 0.0275$, $U_{critical, \alpha(2)=0.05} = 31$]. Only four native

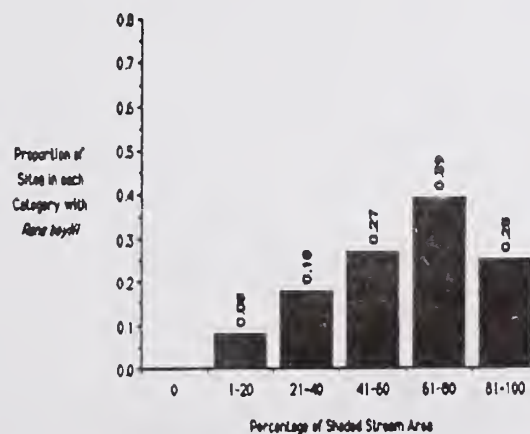


Figure 4.—Histogram of the proportion of sites in stream shading categories where *Rana boylei* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each stream shading category are: 0% ($n=0/5$), 1-20% ($n=3/37$), 21-40% ($n=7/38$), 41-60% ($n=8/30$), 61-80% ($n=9/23$), and 81-100% ($n=2/8$).

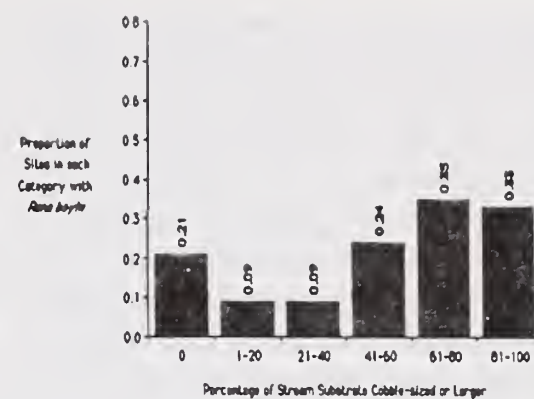


Figure 6.—Histogram of the proportion of sites in substrate categories where *Rana boylei* has been recorded in the Sierra Nevada foothills, California. Sample sizes as a function of the total sample in each substrate category are: 0% ($n=4/19$), 1-20% ($n=3/32$), 21-40% ($n=2/23$), 41-60% ($n=7/29$), 61-80% ($n=9/26$), and 81-100% ($n=4/12$).

fishes, California roach, Sacramento sucker (*Catostomus occidentalis*), Sacramento squawfish (*Ptychocheilus grandis*), and rainbow trout (*Salmo gairdnerii*), occurred with *R. boylei* at more than three of the 29 sites where the latter was recorded, and of these, only California roach occurred with *R. boylei* at more than 50% of the sites where *R. boylei* was recorded. Only one species assemblage, that consisting of California roach, Sacramento squawfish, and Sacramento sucker, occurred with *R. boylei* more often than expected by chance alone (table 7). Correlation analysis indicated that the abundance of 10 of the 12 co-occurring species was significantly inversely correlated with the abundance of *R. boylei* (table 8).

DISCUSSION

Habitat Variation

California Red-Legged Frog

A dense vegetation close to water level and shading water of moderate depth are habitat features that appear especially important to California red-legged frogs. Previous authors have suggested or implied the occurrence of at least one of these habitat features. Storer (1925) noted

that *R. a. draytonii* in streams was restricted to large pools, which implies a moderate water depth. Stebbins (1966, 1985) emphasized vegetative cover as important to red-legged frogs, but his comments confound habitat characteristics that may be attributable to northern versus California (southern) red-legged frogs; data on these two forms should remain partitioned until it is well-established that they are not different species (Hayes and Miyamoto 1984, Hayes and Krempels 1986). Zweifel (1955) coupled the water depth and vegetation features of California red-legged frog habitat, but he emphasizes a herbaceous shoreline vegetation. Our data indicate that a more complex vegetation is a feature of sites where *R. a. draytonii* occurs. Cattails, bulrushes, and shrubby wil-

Table 5.—Spearman rank correlation between selected environmental variables and the coded abundance of *R. boylei* as measured by Moyle (1973). Sample size for each variable is $n = 130$. A double asterisk () indicates significant correlations, based on a critical $r_s = 0.267$ at an α (two-tailed) = 0.002, adjusted for 24 comparisons (13 below and 11 in table 8; see methods).**

Variable	Correlation coefficient (r_s)
Human alteration	-0.160
Vegetation	
Aquatic vegetation (%)	-0.157
Floating vegetation (%)	-0.169
Shade (%)	0.219
Stream morphology	
Pools (%)	-0.205
Riffles (%)	0.304**
Runs (%)	-0.020
Stream substrate	
Mud (%)	-0.035
Sand (%)	-0.085
Gravel (%)	-0.032
Rubble (%)	0.071
Boulder/Bedrock (%)	0.192
Rubble/Boulder/Bedrock (%)	0.172

Table 6.—Occurrences of aquatic macrofaunal species among the 130 stream sites sampled by Moyle (1973) and Moyle and Nichols (1973). Co-occurrences is the number of sites *Rana boylei* was found to co-occur with each species. Percentage of co-occurrences is co-occurrences as the percentage of those sites at which either *R. boylei* or the state species occur. An asterisk (*) indicates introduced species. Ten other fish species (Goldfish (*Carassius auratus*), Prickly sculpin (*Cottus asper*), Common carp (*Cyprinus carpio*), Threadfin shad (*Dorosoma petenense*), Threespine stickleback (*Gasterosteus aculeatus*), Yellow bullhead (*Ictalurus nebulosus*), Redear sunfish (*Lepomis microlophus*), Chinook salmon (*Onchorhynchus tshawytscha*), Brown trout (*Salmo trutta*)) were recorded at low numbers of stations (≤ 8); none were recorded as co-occurring with *R. boylei*.

Species	Occurrences (n =)	Co-occurrences (n =)	% of co-occurrences
Bullfrog (<i>Rana catesbeiana</i>)*	68	2	2
Green sunfish (<i>Lepomis cyanellus</i>)*	61	2	2
Sacramento sucker (<i>Catostomus occidentalis</i>)	55	13	18
Sacramento squawfish (<i>Ptychocheilus grandis</i>)	48	12	18
California roach (<i>Lavinia symmetricus</i>)	43	17	31
Largemouth bass (<i>Micropterus salmoides</i>)*	41	0	0
Mosquitofish (<i>Gambusia affinis</i>)*	37	1	2
Bluegill (<i>Lepomis macrochirus</i>)*	33	3	5
Rainbow trout (<i>Salmo gairdnerii</i>)	27	11	24
White catfish (<i>Ictalurus catus</i>)*	13	1	2
Golden shiner (<i>Notemigonus crysoleucas</i>)*	13	0	0
Hitch (<i>Lavinia exilicauda</i>)	12	1	3
Hardhead (<i>Mylopharodon conocephalus</i>)	11	2	5
Smallmouth bass (<i>Micropterus dolomieu</i>)*	9	3	9

Table 7.—Frequencies of species assemblages of aquatic macrofaunal vertebrates co-occurring with *R. boylei* from data recorded by Moyle (1973). Assemblages listed include only combinations of species recorded as co-occurring with *R. boylei* at least seven localities (see table 6). Listed species are California roach (RCH), Sacramento sucker (SKR), Sacramento squawfish (SQ), and Rainbow trout (RT). Asterisks () identify assemblages co-occurring at frequencies significantly higher than expected by chance, based on a critical $X^2_{df=1, \alpha=0.005} = 7.879$, adjusted for 11 combinations (see methods). Probabilities (p) are those associated with calculated X^2_o values.**

Species assemblage	Frequencies		X^2_o	Probability
	Observed	Expected		
RCH/RT/SKR/SQ	2	1.20	0.077	0.75 < p < 0.90
RCH/SKR/SQ	9	3.15	9.068**	0.003
RCH/RT/SQ	2	2.67	0.011	0.90 < p < 0.95
RCH/RT/SKR	2	2.89	0.053	0.75 < p < 0.90
RT/SQ/SKR	2	2.04	0.104	0.50 < p < 0.75
RCH/RT	5	6.45	0.139	0.50 < p < 0.75
RCH/SKR	10	7.62	0.463	0.25 < p < 0.50
RCH/SQ	9	7.03	0.305	0.50 < p < 0.75
RT/SKR	3	4.93	0.415	0.50 < p < 0.75
RT/SQ	3	4.55	0.243	0.50 < p < 0.75
SKR/SQ	11	5.38	4.959	0.026

lows, the plants comprising emergent and shoreline vegetation at such sites, typically shade a substantial surface area of water with a dense matrix at or near water level. California red-legged frogs appear sensitive to the presence of such a vegetation structure because most sites from which frogs were recorded lacked significant alteration of emergent or shoreline vegetation (see table 2). Moreover, because only juvenile frogs were recorded from most sites with limited shoreline or emergent vegetation, a minimum amount of such vegetation appears to be needed for survival of adults. Parallel arguments apply to water depth. Previous authors have characterized *R. a. draytonii* as a pool- or pond-dwelling species (Stebbins 1966, 1985; Storer 1925; Zweifel 1955) and descriptions corresponding to that characterization were recorded for this frog at most sites. Yet, we found that using minimum water depth was a more encompassing habitat descriptor be-

cause it included canals and stream sites where adult frogs were described as being common and that had the minimum water depth requirement, but could not be described as either ponds or stream pools. Available description of such sites indicates that they fit the definition of a run (Armour et al. 1983), although data upon which part of the definition is based (the rate of water flow) are lacking.

We believe that California red-legged frogs occur primarily in streams because alternative sites (ponds) that have suitable water depth and vegetation characteristics were historically rare outside of stream habitats rather than because red-legged frogs are somehow pre-adapted for survival in streams. Historically, pond habitats below 1500 m in the Central Valley were mostly vernal pools, a habitat too shallow and ephemeral to develop the macrovegetation found associated with *R. a. draytonii* (see Holland 1973, Jain

1976). Even the only two exceptions to *R. a. draytonii* not occurring in vernal pools support this hypothesis. A large vernal pool in San Obispo County, California is known to have a population of California red-legged frogs (D. C. Holland, pers. comm.). However, this vernal pool is atypical because it possesses significant macrovegetation and water depth. These features appear to be present because this large (ca. 20 ha) pool does not dry down each year. The second exception is a vernal pool in coastal southern California in which two frogs with abnormal numbers of legs were found (Cunningham 1955). Cunningham thought that the defects were induced by exposure to high temperatures during early development, a condition facilitated by the limited vegetative cover that was present. His speculation may be valid if California red-legged frog embryos have a low critical thermal maximum (Hayes and Jennings 1986). Storer (1925) thought that *R. a. draytonii* was excluded from temporary (vernal) pools because its larval period is relatively long, but the more likely mechanism is that frogs immigrating to such pools were unable to establish because suitable habitat was lacking. The latter hypothesis is supported because California red-legged frogs are not recorded from the many vernal pools that hold water for intervals longer than the minimum time required by *R. a. draytonii* to complete metamorphosis (10 weeks; Hayes, unpubl. data; see also Jain 1976, Zedler 1987).

Rana a. draytonii also appears to have responded to the creation of habitat with the appropriate vegetation and water depth characteristics. A significant aspect of the changes in aquatic habitats that have occurred in the Central Valley below 1500 m is an increase in the number of permanent ponds (Moyle 1973). Storer (1925) reported that *R. a. draytonii* occurred in a number of water storage reservoirs and artificial ponds, but the habitat features of those sites

Table 8.—Spearman rank correlation between the numerical (non-coded) abundance of the vertebrate macrofauna and the abundance (coded) of *R. boylei* as recorded by Moyle (1973). Sample size is based on the total number of sites where either *R. boylei* or the species being compared was present. A single asterisk (*) indicates introduced species. A double asterisk (**) identifies significant correlations at an α (two-tailed) = 0.002, adjusted for 24 comparisons (11 below and 13 in table 5; see methods). Probability (p) is the probability of obtaining the calculated Spearman correlation coefficient (r_s). Common names for the listed species are in table 6.

Species	Sample size (n =)	Correlation coefficient (r_s =)	Probability (p =)	Critical r_s
<i>Catostomus occidentalis</i>	71	-0.404**	<0.001	-0.363
<i>Gambusia affinis</i> *	62	-0.835**	<0.001	-0.388
<i>Ictalurus catus</i> *	41	-0.798**	<0.001	-0.473
<i>Lavinia exilicauda</i>	40	-0.760**	<0.001	-0.479
<i>Lavinia symmetricus</i>	55	-0.316	0.020	-0.411
<i>Lepomis cyanellus</i> *	88	-0.742**	<0.001	-0.327
<i>Lepomis macrochirus</i> *	59	-0.827**	<0.001	-0.397
<i>Micropterus dolomieu</i> *	35	-0.538**	0.001	-0.510
<i>Mylopharodon conocephalus</i>	38	-0.607**	<0.001	-0.491
<i>Ptychocheilus grandis</i>	66	-0.541**	<0.001	-0.376
<i>Rana catesbeiana</i> *	90	-0.800**	<0.001	-0.323
<i>Salmo gairdnerii</i>	44	-0.425	0.005	-0.458

were not described. Thus, it was of special interest to find that no significant difference could be identified between the probability of extinction of *R. a. draytonii* at substrate-altered sites (mostly small impoundments) and at sites lacking such alteration. Moyle (1973) concluded that the decline of *R. a. draytonii* was related in part to human-induced alteration, including creation of impoundments. Our data suggest that human-induced alteration creating small impoundments cannot be related directly to the disappearance of California red-legged frogs. We emphasize that these data do not exclude the alternative, discussed later, which indicates that the creation of small impoundments is likely to have an indirect negative effect on *R. a. draytonii* by facilitating the dispersal of introduced aquatic predators.

Besides features of habitat structure associated with *R. a. draytonii*, its isolation from one or more aquatic macrofaunal predators is the other key element suggested by these data. No significant variation was found in the features of habitat structure important to *R. a. draytonii* between intermittent and perennial aquatic sites, so differences in habitat structure cannot explain why *R. a. draytonii* is recorded most frequently from intermittent aquatic sites. We believe that California red-legged frogs were recorded most frequently from intermittent sites because the likelihood of extinction at perennial sites is now higher than at intermittent sites (see table 4) and few historical data are available from when frogs were often found at perennial sites.

California red-legged frogs are now extinct from all sites on the Central Valley floor, all of which were perennial and, except for one, were recorded prior to 1950. We believe that the disadvantage associated with perennial sites and the advantage associated with intermittent sites is the degree to which the former allow, and the latter restrict, the

access of aquatic macrofaunal predators.

The remaining variation in features of *R. a. draytonii* habitat we have identified can be directly, or indirectly, linked to a hypothesis invoking the influence of one or more aquatic macrofaunal predators. The significantly lower likelihood of extinction at sites with small drainage areas (table 4) and *R. a. draytonii* being recorded from a greater number of localities with smaller drainage areas (fig. 1) and lower stream orders (fig. 2), are probably unrelated to either drainage area or stream order effects per se. Rather, they are a function of both the bias against recording historical data and the fact that sites with smaller drainages or lower stream orders have a higher probability of being intermittent aquatic habitats, which have a higher probability of excluding aquatic predators. Limited co-occurrence with aquatic predators, namely bullfrogs and predatory fishes, and a significantly higher likelihood of extinction at sites where bullfrogs were recorded (table 4) may indicate a negative interaction with one or more of these species. *Rana a. draytonii* did not co-occur with any fish species frequently. It co-occurred most often with California roach, a small, omnivorous native fish that is thought to have declined, in part, due to predation by introduced fishes (Moyle and Nichols 1974, Moyle 1976). We did not detect a significantly higher likelihood of extinction at sites with introduced fishes. However, the sample was too small to partition to permit testing individual fish species, the level at which we believe such an effect is most likely.

While we are reasonably convinced that the greater restriction of *R. a. draytonii* to intermittent aquatic habitats is an effect due to novel aquatic predators, we emphasize that these data cannot identify which are the aquatic predators producing such an effect. The inability to identify the responsible predators is complicated

by the condition of limited overlap between each potential predator and *R. a. draytonii*. That condition prevents excluding the alternative that different habitat requirements rather than any predatory interaction may explain the limited overlap in habitat use between each putative predator and California red-legged frogs (compare Moyle 1973 for bullfrogs and Moyle and Nichols (1973) for various fishes, but especially mosquitofish and green sunfish; see also Hayes and Jennings 1986 for a discussion). It is this fact and the apparent intolerance of *R. a. draytonii* to unshaded habitat that leads us to suggest that some alteration of riparian vegetation may be necessary to create the conditions for a negative interaction.

Foothill Yellow-Legged Frog

Partly shaded, shallow streams and riffles with a rocky substrate that is at least cobble-sized are the habitat features that appear to be important to foothill yellow-legged frogs. Previous authors agree that *R. boylei* occurs in streams (Moyle 1973; Stebbins 1966, 1985; Storer 1925; Zweifel 1955), but variation exists in the features of streams associated with these frogs. Of environmental variables that appear important to *R. boylei*, the percentage of stream area in riffles is the only one we were able to correlate significantly, albeit weakly, with its abundance. Moyle (1973) obtained a similar positive correlation in his original analysis of the same data, and Stebbins (1966, 1985) also emphasized riffles as one of the key aspects of *R. boylei* habitat. The reason for the weak correlation we found is uncertain, but one or more of three factors probably produced that result. First, as intermittent streams lose surface flow during late summer, riffles disappear, and *R. boylei* can then be found associated with stream pools (Fitch 1938, Slevin 1928, Storer 1925, Zweifel 1955).

Moyle's data were collected in late summer and 10 of the 29 stream sites at which *R. boylei* was recorded were intermittent, so data from these sites may have diluted the correlation. Second, riffle area may be correlated with the abundance of *R. boylei* only above or below certain values (see fig. 5). Lastly, *R. boylei* has been reported from sites with little or no riffle habitat unrelated to seasonal patterns (Fitch 1938, Zweifel 1955).

Apart from riffles, our reanalysis of environmental variables differs from that of Moyle (1973), who found that five of the other variables that we re-examined were either positively (i.e., shading and boulder/bedrock; compare table 1 in Moyle [1973] and our table 5) or negatively (i.e., rooted vegetation [= our aquatic vegetation], pools, man modified [= our human alteration]) significantly correlated with the abundance of *R. boylei*. We attribute this difference, in part, to our analysis being more conservative because we adjusted α for the experimentwise error rate, our analysis was not restricted to localities where only frogs were found, and we used non-parametric tests. Some of the correlations that Moyle (1973) observed with *R. boylei* abundance may have been significant due to one or more of these differences. We must emphasize, however, that several of the variables that Moyle found correlated with *R. boylei* abundance vary differentially in their occurrence between riffles and pools (e.g., boulder/bedrock; see Moyle [1973] and Moyle and Nichols [1973]). Those variables are also susceptible to the seasonal correlation-altering effects discussed for the riffle variable. Thus, a conservative analysis, like ours, is less likely to detect variables related to frog abundance within such a data set.

Nevertheless, variables identified as important to *R. boylei* need not be correlated to its abundance. Stream depth, shading, and substrate type may represent such variables. Our reanalysis of Moyle's data suggests

that sites with a shallow average stream depth are somehow advantageous (see fig. 3). Moyle (1973) found no significant correlation between the abundance of *R. boylei* and stream depth, and he did not discuss stream depth with respect to foothill yellow-legged frogs in any other context. Zweifel (1955) noted that streams in which *R. boylei* occurred were seldom more than 0.3 m deep, and Fitch (1936), Storer (1925), and Wright and Wright (1949) found that *R. boylei* usually lays eggs in shallow water. Still, overall importance of stream depth to *R. boylei* remains unclear. Our reanalysis also suggests that some advantage is linked to increased shade up to some intermediate level (see fig. 4). Zweifel (1955) described shading in typical *R. boylei* habitat as interrupted, whereas Moyle (1973) reported a positive correlation between frog abundance and the degree of shading.

Some workers have emphasized the degree of openness or insolation in *R. boylei* habitat, rather than addressing shading (Fitch 1938; Stebbins 1966, 1985). Nevertheless, even the latter imply that some shading is present. Fitch's (1938) suggestion that yellow-legged frogs are excluded by dense canopy may be supported by Moyle's data because he recorded no *R. boylei* at sites with >90% shading (see also fig. 4). Our reanalysis also suggests that some advantage is associated with sites possessing at least a cobble-sized substrate (see fig. 6). Although workers have most frequently emphasized the rocky aspect of *R. boylei* habitat (Fitch 1936, 1938; Moyle 1973; Stebbins 1966, 1985; Storer 1925), substrate descriptions of that habitat are probably as varied as any other single variable. Moyle (1973) identified a positive correlation between the percentage of stream area with bedrock and boulders and the abundance of *R. boylei*, yet sites with gravelly (Gordon 1939), sandy (Zweifel 1955), or muddy substrates have also been recorded (Fitch 1938, Storer 1925). Because

Moyle's data do not provide frog age, we could not determine whether sites having a substrate that was less than cobble-sized were simply marginal habitat with juvenile *R. boylei* (see Zweifel 1955), or whether they represented real variation in habitat used by established populations.

Fitch (1938) and Zweifel (1955) reported on a few sites with adult frogs that lacked a substrate that was cobble-sized or larger and appeared to have few predators. They suggested that yellow-legged frogs are rarely recorded from such sites because their predators may access the "atypical" habitat more easily. Nevertheless, data on the aforementioned variables reinforce the conclusion already arrived at with *R. a. draytonii*: Existing data cannot distinguish hypotheses explaining the differential occurrence of *R. boylei* among habitat categories due to mechanistic or physiological restriction (i.e., "habitat preference") from hypotheses invoking habitat restriction because of some novel predator (Hayes and Jennings 1986). The data for *R. boylei* differ from that of *R. a. draytonii* in that we cannot confidently reject the alternative that no restriction is occurring. For example, it remains unclear whether earlier reports of "atypical" habitat use by *R. boylei* were simply rare occurrences, or whether those instances actually reflect a general pattern of broader habitat use in years prior to when Moyle (1973) obtained his data, indicating that habitat restriction had occurred.

Management Implications

Both *R. a. draytonii* and *R. boylei* need immediate management consideration if many remaining populations are to survive into the next century. *Rana a. draytonii* is extinct on the floor of the Central Valley, and is probably extinct from over half of the drainage systems in the Central Valley from where it was historically recorded. We consider many of the

remaining populations at risk since over half of the localities are within areas projected to be flooded by reservoirs proposed for the Coast Range slope of the Central Valley (Wernette et al. 1980; C. J. Brown, Jr., pers. comm.). Populations at an additional 10 localities are at an unknown, but probably high level of risk. Although these additional localities will not be flooded by the proposed reservoirs, flooding will isolate the frogs present in small (<10 km²) drainage basins upstream of the reservoirs. We lack data on how isolation in very small drainage basins may increase the probability of extinction (see Fritz 1979), but the only four localities isolated by reservoirs for which data exist now lack red-legged frogs (Hayes, unpubl. data). California red-legged frogs were recorded at each of the latter sites up to 20 years ago, between one and five years after flooding of the adjacent reservoir had taken place. Comparable data on the decline of *R. boylei* in the Central Valley are lacking, but observations by experienced workers indicate that *R. boylei* no longer occurs at many localities in the Central Valley drainage basin where it was historically recorded (Moyle 1973; R. Hansen, D. Holland, S. Sweet, D. Wake, pers. comm.; Jennings, unpubl. data).

Modal habitat requirements for both frog species suggested by existing data should be given special attention in any management attempt. Since our comments here are based on data for both species in the Central Valley of California, attempts to apply the management recommendations we make to other areas within the geographic range of each species should be done cautiously. We cannot overemphasize that preservation of what appears to be the preferred (modal) habitat condition for either species should be stressed where it is ambiguous whether restriction is due either to the negative impact of the introduced aquatic macrofauna, or to intrinsic mechanical or physiological limitations. Preservation of non-mo-

dal habitat is not only likely to incur a greater cost to ensure frog survival, but more importantly, it may still not allow survival if the worst-case scenario (restriction of habitat by the introduced aquatic macrofauna) is true.

The modal habitat features of *R. a. draytonii* and *R. boylei* are similar in two ways. First, the aquatic habitat of each has some shading. Yet, shading associated with California red-legged frogs differs because of the apparently crucial aspect of having dense vegetation at or near water level. We lack details on just how the streams Moyle (1973) sampled were shaded, but knowledge of some of the species providing shade suggests that a higher overstory was typical. *Rana a. draytonii* will always be at greater risk than *R. boylei* where alteration of riparian vegetation is a problem simply because of its shade requirement; even altered stream environments may retain some shading, but a lesser probability will always exist that the shading that remains will have the structure needed by *R. a. draytonii*. Second, each species occurs most frequently in the absence of any aquatic macrofauna, and both species have probably experienced some habitat restriction due to introduced aquatic predators. Only one small native minnow co-occurs at over one-third the sites where each frog species was recorded, and even that species was not positively correlated with frog abundance. For *R. a. draytonii*, the data are reasonably convincing that restriction has occurred away from perennial aquatic sites. For *R. boylei*, data do not clearly indicate habitat restriction. Still, the fact that *R. boylei* was found at fewer intermittent sites leads us to believe that if habitat restriction has taken place, it has occurred away from intermittent aquatic sites. We reason that since riffles disappear seasonally in intermittent streams, such streams lack the condition found in perennial streams that may be an advantage if

riffle habitat is a refuge, i.e., that perennial streams have riffle habitat year-round.

Our analysis indicates that attempts at management of these two frogs should address at least three other habitat variables: water depth, stream morphology, and substrate type. *Rana boylei* appears to require a shallow water depth of <0.6 m, whereas *R. a. draytonii* seems to require some water \geq 0.7 m deep. Data on stream morphology and substrate type, which were recorded only for *R. boylei*, suggest that both of a percentage of riffle area and at least cobble-sized substrate of greater than 40% best suit this species. Parallel data for *R. a. draytonii* are lacking, but since data on other habitat parameters measured for *R. a. draytonii* are largely "reciprocals" of the correlates of riffle habitat associated with *R. boylei*, we anticipate that some relationship to the more lentic water stream morphology categories (i.e., pools and runs) and their associated finer substrate categories (i.e., silt and sand) will be demonstrated for *R. a. draytonii*.

Experiments may ultimately identify the introduced aquatic predators likely responsible for the declines of these frogs, but management based on current knowledge should address no less than the worst-case scenario; i.e., that any member of the introduced aquatic macrofauna presents a risk to the survival of populations of *R. a. draytonii* and *R. boylei*. Thus, the sound management decision is to implement measures that will maximize the degree of isolation between existing populations of each frog species and any members of the introduced aquatic macrofauna. Just how isolation should be maintained will vary depending on the site considered, but some general suggestions can be made. First, passive measures promoting isolation are preferable because they are less costly and are less likely to affect non-target species. Simply avoiding habitat modification where the mo-

dal habitat features for each frog species already exist is a passive measure that will provide some degree of within-habitat isolation since members of the introduced aquatic macrofauna show little overlap in their habitat requirements with each frog. Yet, populations of either frog species currently coexisting in a habitat mosaic with members of the introduced aquatic macrofauna may still be doomed. This possibility leads us to suggest that most efforts at management should be spent on frog populations at sites that currently lack introduced aquatic predators. We consider protection of the entire hydrographic basins of drainage systems tributaries (see methods for definition) an important part of such management attempts because intrusion by introduced aquatic predators is probably most easily controlled if the only natural access route is via upstream movement. To our knowledge, no locality within the Central Valley drainage area having an extant California red-legged frog population has its entire hydrographic basin protected. Moreover, only two California red-legged frog populations within this area occur at sites where the habitat is currently offered some protection. Second, isolation strategies may differ depending on whether proximate populations of introduced aquatic predators are bullfrogs or fishes or both. Apart from being physically transported, fishes are effectively prevented from moving upstream by a barrier (see Hayes and Jennings 1986), whereas bullfrogs, capable of overland movement under wet conditions (Hayes and Warner 1985), are less likely to be barrier-limited. We indicated earlier that creation of small impoundments may enhance the ability of *R. a. draytonii* to establish at certain sites through the creation of features found in its habitat, but attention to the positioning of such impoundments is an equally important consideration. If impoundments are close enough that bullfrogs reach

them from an adjacent source population, such sites can also act as local refuges at which new bullfrog populations can become established, and can serve as new focal points from which to disperse. Moreover, new impoundments probably favor the establishment of bullfrogs simply because their unvegetated condition more closely matches the habitat recorded for bullfrogs (Moyle 1973). These arguments simply indicate that particular attention should be given to avoiding the creation of "stepping-stone" pathways, i.e., provision of access into currently isolated drainages by the positioning of impoundments that permit introduced predators, like bullfrogs, to encroach progressively by dispersal.

The limits of our analysis indicate that significant aspects of habitat variation for both frog species remain to be understood. In particular, an understanding is needed as to how key variables influence reproduction and refuge sites. Although available data on oviposition patterns suggest a link between *R. a. draytonii* and the presence of emergent vegetation (Hayes and Miyamoto 1984), and *R. boylei* and a rocky substrate (Fitch 1936, 1938; Storer 1925; Zweifel 1955), it is unclear for either species to what degree the substrate can vary before oviposition may be prevented and also how aspects of reproduction besides oviposition may be linked to habitat variation. Perhaps the most crucial gap is a lack of understanding of what aspects of habitat variation are related to frog refuge sites, including the often temporary refuges used as an escape from predators as well as those refuges used during the season of inactivity. The former type of refuge site may be related to the deep-water and dense vegetation habitat associated with *R. a. draytonii*, and the riffle habitat associated with *R. boylei*, but what aspects of those habitat features really comprise the refuge and to what degree they may vary before they are no longer a ref-

uge is unknown. A understanding of the latter is pivotal to the identification of predator-induced habitat restriction. Most importantly, an understanding of how reproduction and refuge sites are related to habitat variation for these two frogs is essential if management is to ever be refined to a level where habitat variables, either individually or in concert, may be manipulated. Finally, if habitat manipulations are attempted, they will have to be implemented with caution in aquatic systems where both *R. a. draytonii* and *R. boylei* co-occur; differences in habitat characteristics between each species suggest that whatever way one or more of several habitat variables are manipulated, they will probably result in a tradeoff between habitat losses and habitat gains for *R. a. draytonii* versus *R. boylei*.

In summary, habitat analysis for the two ranid frogs, *R. a. draytonii* and *R. boylei*, indicates that each species is most frequently associated with discernibly different aquatic habitats, the former with densely vegetated, deep water and the latter with rocky, shallow-water riffles in streams. The species are similar in that they infrequently co-occur with any aquatic vertebrates, especially the introduced aquatic macrofauna. Low levels of co-occurrence between frogs and the introduced aquatic macrofauna have two confounded explanations: 1) preferential use of different habitats between the introduced aquatic macrofauna and frogs, and 2) habitat restriction because frogs and their life stages are preyed upon by the introduced aquatic macrofauna. However, even though it is presently impossible to identify the responsible predator, temporal data strongly suggest that *R. a. draytonii* has been restricted by some introduced aquatic predator and the same possibility cannot be excluded for *R. boylei*. For both species, a management scheme is necessary to avert existing trends of decline, and ultimately, extinction. A management

scheme that minimizes the risk of extinction based on current data must address the worst-case scenario among the alternatives implicated in limiting frog distributions. To address anything less increases the risk of extinction if that alternative is true. Since that alternative is habitat restriction by an introduced aquatic macrofauna, management should strive to isolate both frog species from the introduced aquatic macrofauna. Moreover, available data indicate that preservation of modal conditions for habitat variables identified as associated with each species is a suitable interim strategy, since it is more likely to promote isolation. Significant refinements of this management scheme will require a thorough understanding of how habitat variables associated with each frog species are linked to their refuge requirements and their reproductive patterns.

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Integrating Anuran Amphibian Species into Environmental Assessment Programs¹

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As a result of our increased understanding of the roles of wildlife species in ecosystem structure and function, and legal requirements to develop holistic approaches to environmental management, it has become increasingly common to include all species of wildlife in resource inventories and monitoring programs (Chalk et al. 1984). However, amphibians are often ignored or given minimal attention in such programs, even though they are important wildlife resources and should be given serious consideration in management evaluations (Bury and Raphael 1983, Bury et al. 1980, Jones 1986). If included in resource evaluations at all, amphibians are usually lumped with reptiles in a category called herpetofauna and even then are often only represented as items in a species list.

This is unfortunate because, in addition to their ecological importance, anurans are potentially valuable as a unique form of indicator species capable of integrating environmental changes occurring in both the terrestrial and aquatic phases of their habitats. Furthermore, because they occupy small ponds and the shallow margins of lakes, anurans

are likely to be the first vertebrates to come in contact with contaminated run-off or acidified snowmelt. This could make them useful as elements of an early warning system for the detection of environmental contamination. Campbell (1976) found that the boreal toad, *Bufo boreas*, would be an especially effective indicator species for monitoring the impact of cloud seeding in the mountains of Colorado. It is also significant that many anurans require specialized habitats in wetland areas and riparian zones, and could serve as indicator species for the overall health of these areas of special ecological importance.

Despite their potential usefulness, there are several reasons why amphibians are not given adequate at-

Abstract.—Anurans are often given minimal attention in environmental assessments despite their ecological importance and potential value as indicator species. Habitat and guild-based models must be adapted to include all life cycle stages of anurans. A preliminary habitat suitability model for the American toad shows how this can be accomplished.

tention in environmental assessments. The importance of amphibians in ecosystems is generally unrecognized, particularly by the general public and the resource managers who must respond to the desires of this public as they set management priorities. Also, the secretive habits during the non-breeding season, and complex life cycles of amphibians make them relatively difficult to study. Consequently, the natural history of many amphibian species is not well known. Another factor is that current models for monitoring and assessment have been developed for either terrestrial or aquatic species and have not been adapted to species with divergent life cycle stages which depend on both aquatic and terrestrial habitats (table 1).

Table 1.—Habitat components and life cycle stages of anurans.

Habitat component	Eggs/Pre-feeding tadpoles	Feeding tadpoles	Metamorphosing tadpoles	Juveniles	Adults
Aquatic Phase					
Spawning sites	X				
Tadpole habitat	X	X	X		
Aquatic/Terrestrial Interface Phase					
Tadpole habitat			X		
Juvenile habitat			X	X	
Terrestrial Phase					
Summer habitat				X	X
Hibernation sites				X	X
Movement corridors				X	X
Interspersion Factors					
Distribution of habitat components					X X
Density of habitat components					X X

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Approaches for incorporating wildlife into resource evaluations include inventories of relative abundance and species richness, development of databases, the use of indicator species, and the development of species diversity indices and models using guild concepts. However, the application of these approaches to species of Amphibia has not kept pace with applications to other species of vertebrates.

The primary purpose of this paper is to suggest ways to use single species models, and models which use guilds and habitat structure, to more effectively integrate anuran amphibians into resource assessments. A single species model for the American toad, stressing the importance of tadpole habitat, is presented in some detail.

Models for Anurans

Guilds and Habitat Structure

Guild-based environmental assessments are especially useful from an ecological perspective, although they are most effective when used in combination with other methods (Karr 1987). Unfortunately, when amphibians are included in guild-based programs they are usually considered too simplistically. A common procedure is to categorize them according to their general spawning and feeding habitat, but to include no further detail (e.g. see Thomas et al. 1979).

The habitat models developed for Arizona (Short 1984) represent a good starting point for producing effective models for anurans. In these models wildlife guilds are used to correlate habitat use with habitat structure (layers) by associating a species with a particular plant community (habitat or cover type), and then with a habitat layer. Layers of both terrestrial and aquatic habitat are included.

This system is as appropriate for terrestrial adult anurans as it is for any small, terrestrial vertebrate. However, the aquatic phases of the model require further development if it is to be used with the aquatic larval stages of amphibians. The adaptive significance of the tadpole stage has been established by Wassersug (1975) and Wilbur (1980), and it is clear that the habitat requirements of larval anurans should be an important component of habitat models. The selection of a spawning site that will provide high quality habitat for the tadpole stage is likely to be critical to the evolutionary success of an anuran species.

Single Species Models

Habitat models for indicator species have been developed by the U.S. Fish and Wildlife Service (1981), the U.S. Forest Service (Berry 1986) and others (e.g. Clawson et al. 1984) for use in assessing environmental impacts and in making management decisions. A comprehensive habitat model for an anuran species must encompass spawning sites, tadpole habitat, metamorphic sites, juvenile and adult feeding habitat, movement corridors and hibernation sites. For example, a model developed for the bullfrog (*Rana catesbeiana*) illustrates how the approach can be applied to

Table 2.—Components of habitat for *Bufo americanus* (measurable attribute in parentheses).

Spawning Habitat

- Shallow, ephemeral ponds (depth range)
- Emergent or submergent vegetation (% cover)
- Exposure to direct sunlight (% of area shaded)

Tadpole Habitat

- Ponds with access to shallow shoreline areas (< 10 cm) and to deeper areas (10-100 cm)
- Substrates with food
 - periphyton (% cover)
 - bottom areas with detritus or microorganisms (% cover)
- Microorganisms suspended in water column (density)
- Exposure to direct sunlight (% of area shaded)

Metamorphic Habitat

- Shallow depth gradient at shoreline (< 10 cm)
- Exposure to direct sunlight (% of area shaded)
- Moist substrate on shore (moisture content)
- Vegetative cover on shore (% cover)

Juvenile and Adult Habitat

- Availability of insect and other invertebrate prey (prey density)
- Access to moist substrates and refugia (moisture content and refugia density)
- Access to vegetative cover (distance to cover)

Hibernation Site

- Unoccupied animal burrows (burrow density)
- Friable soils (soil texture)
- Root zones of large trees (large tree density)

Interspersion

- Movement corridors between hibernation and spawning sites (distribution of continuous open areas with adequate cover)
- Distribution and density of potential spawning sites within the home range of the population (density of spawning sites)

an anuran species that is primarily aquatic (Graves and Anderson 1987). While this model is well constructed, a different modeling approach would be needed for anurans with terrestrial adult stages. A limitation of the bullfrog model is that the habitat requirements of the tadpole stage are not given in sufficient detail. This is important because the larval stage (up to three years in duration) represents a significant proportion of a bullfrog's total lifespan.

A different array of habitat components for a species that is predomi-

nantly terrestrial is an adult, the American toad (*Bufo americanus*) is outlined in table 2. This outline is based on extensive field studies in Michigan (Beiswenger 1975, 1977), field observations of related toad species in Oregon and Wyoming (Beiswenger 1978, 1981, 1986), and information found in the literature.

Including the terrestrial features of toad habitat in assessments does not represent a particularly difficult challenge because these features can be described using well-established approaches developed for other small

vertebrates that live on and below the surface of the ground. However, tadpole habitat is also important and must be incorporated into habitat assessment procedures. This is somewhat more challenging because less is known about tadpole ecology and techniques for describing tadpole habitat are not well developed.

A Habitat Model for the American Toad

A preliminary version of a habitat suitability model for the American toad is described here to show how the requirements of all life cycle stages could be incorporated into such a model (figs. 1 and 2). The model includes 10 variables and is based primarily on the author's experience and a partial literature review. Consequently, the model should be refined through a more extensive analysis of the literature and a peer review process before it is field tested.

The habitat requirements of spawning adults and tadpoles are included in the aquatic cover/reproductive component of the model. The quality of spawning sites selected by American toads is influenced by structural features such as depth gradients and vegetation. Adult toads typically lay their eggs in shallow, unshaded, vegetated areas (variables 2 and 3), distributing them in strands on the vegetation. At first the newly hatched tadpoles do not feed, but remain at the site where the eggs were laid.

Older tadpoles are active swimmers and display a variety of feeding modes that are influenced to a large measure by structural features of the habitat (e.g. aquatic vegetation and depth gradients) (variables 1, 2, and 4). Wassersug (1975) has shown that tadpoles are essentially non-discriminant suspension feeders, although they use a variety of means for obtaining food. Tadpoles of the American toad most commonly graze

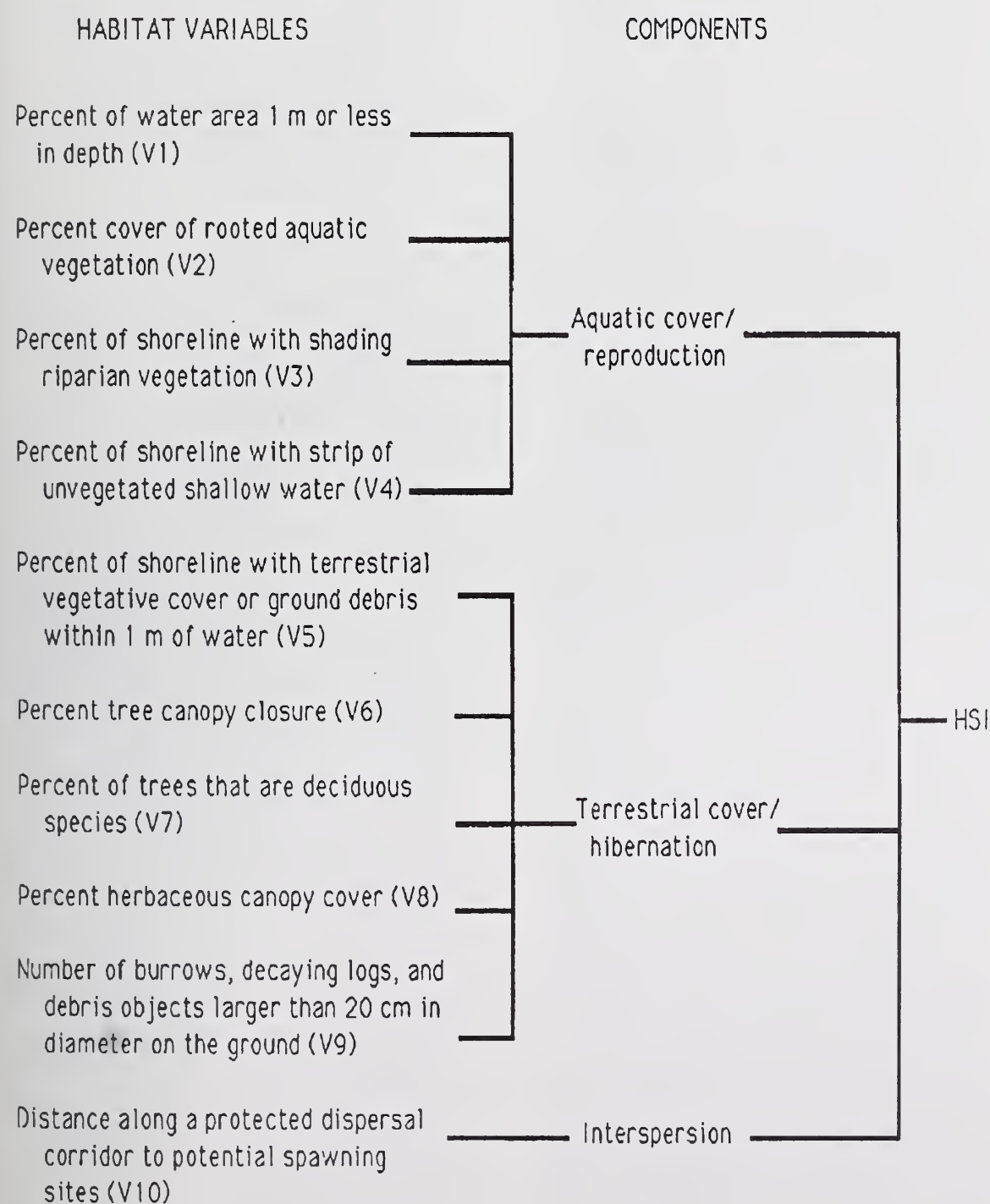


Figure 1.—Relationships of habitat variables to components of an HSI model for the American toad.

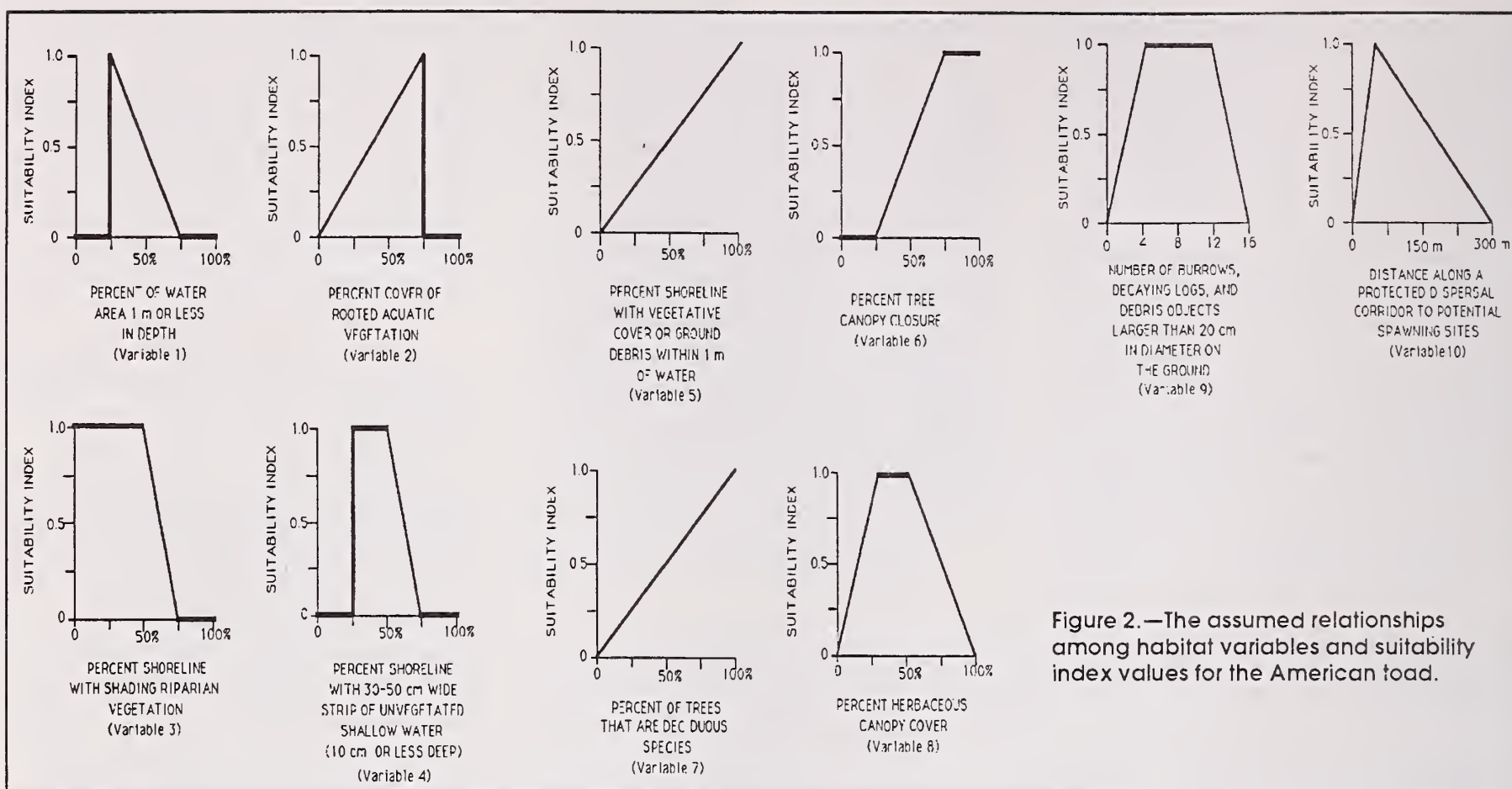


Figure 2.—The assumed relationships among habitat variables and suitability index values for the American toad.

periphyton from emergent or submergent vegetation, or scrape microorganisms and detritus from the pond bottom and other substrates. However, when blooms of suspended algae are present, the tadpoles become midwater filter feeders. They also feed on organic material supported by the surface film of the pond. At other times, the tadpoles are facultatively cannibalistic or coprophagic. The particular feeding mode employed is usually influenced by a combination of factors including the type of food available, depth and temperature gradients, vegetation structure and the degree of social behavior exhibited by the tadpoles (Beiswenger 1975). Most of the time toad tadpoles feed from substrates provided by the structural features of their environment. Diaz-Paniagua (1987) also found structural features of aquatic vegetation to be important in the distribution of the tadpoles of five anuran species in Spain.

Habitat use by tadpoles is strongly influenced by temperature, which in the shallow ponds they occupy is

highly correlated with depth and solar radiation (variables 1, 3, and 4). For example, in northern Michigan ponds were early summer temperatures varied greatly over the diel period, toad tadpoles consistently selected the warmest available water in thermally stratified ponds (Beiswenger 1977). Thus, they occupied the deepest areas of the pond (greater than 50 cm in depth) at night, avoiding the shallow pond margin where temperatures were 5.5 C cooler. During the day tadpoles moved to shallow areas near shore which were 9 C warmer than the deeper areas of the pond. During those times when there was no thermal stratification (e.g. cloudy days), or later in the summer when pond temperatures were uniformly high, the tadpoles used all parts of the pond (Beiswenger 1977). These observations indicate that tadpole habitat quality is partly determined by thermal stratification associated with depth gradients and exposure to direct sunlight.

Habitat quality for metamorphic tadpoles is strongly influenced by

their vulnerability to predation (variables 4 and 5). As Arnold and Wassersug (1978, p. 1019) expressed it, "the transforming anuran is neither a good larva nor a good frog." The larvae develop forelimbs which impede swimming, the tail remnant on the newly emergent juvenile interferes with its jumping ability. Consequently, the availability of structural features such as hiding cover and moist substrates is important for the successful emergence and dispersal of metamorphosing tadpoles.

Habitat quality for juvenile and adult toads is determined by factors generally associated with deciduous or mixed coniferous/deciduous forests. These factors include moderate temperature regimes, invertebrate prey density, protected microhabitats with moist substrates, vegetative cover, and access to hibernation sites. Some of the variables used as surrogate measures of substrate moisture and other forest floor conditions in the HSI model for the red-spotted newt (Sousa 1985) were adapted for the American toad model (variables 6, 7, and 8). Juvenile and adult toads

also need moist cover during hot dry periods and for winter hibernacula. These can be provided by soils which are suitable for burrowing, existing small mammal burrow systems, or decaying logs and other debris objects on the ground (variable 9).

The American toad model includes interspersions as a habitat-related factor. Movement corridors interconnecting spawning areas, summer habitat and hibernation sites are an important component of juvenile and adult habitat (variable 10). Brode and Bury (1984) have pointed out (cited in Ohmart and Anderson 1986), that such corridors are important for dispersal and genetic continuity, and anurans use riparian zones as travel lanes. Habitat fragmentation by road construction (Rittschof 1975), or other forms of habitat destruction can disrupt these travel lanes and prevent anurans from reaching spawning ponds or hibernation sites.

Attention must also be paid to other aspects of interspersions. For example, the reproductive success of toads depends on the continuing availability of shallow water habitats. Ponds with optimum spawning conditions in a given year may be dry in years with low precipitation, or too deep in years when flooding prevails. At the same time, changing water levels may result in the availability of new spawning sites. Apparently in response to this kind of variation, some species of toads do not use the same spawning site every year (Kelleher and Tester 1969) and in some years may not breed at all. Because of variation like this, it is important to describe the distribution of habitat components, such as spawning sites and movement corridors, in a broad geographic area and over a range of environmental conditions.

Relationships among the habitat variables and habitat components are expressed by equations in HSI models. A value for the aquatic cover/reproduction (SIA) component is obtained by combining the suitability

index values for variables 1 through 4, as shown in the following equation.

$$SIA = SIV1 \times SIV2 \times \frac{(SIV3 + SIV4)}{2}$$

This assumes that the suitability of aquatic habitats is primarily determined by the presence of water depths ranging from less than 10 cm to 1 m, rooted aquatic vegetation to provide cover and substrates for food, and shallow, unshaded shoreline areas.

It is assumed that terrestrial habitat suitability (SIT) is determined by the availability of cover with moist substrates, invertebrate prey and hibernation sites. The following equation shows how these habitat values could be evaluated using variable 5 to assess cover for metamorphic stages, 6, 7, and 8 as surrogate measures of substrate moisture, and variable 9 for the availability of hibernacula.

$$SIT = \frac{(SIV5 + SIV6 + SIV7 + SIV9)}{4}$$

Overall habitat suitability (HSI) is determined by combining the suitability values for the aquatic (SIA) and terrestrial (SIT) habitat components with the suitability value for interspersions (SII) as shown in the following equation.

$$HSI = (SIA \times SIT \times SII)^{1/3}$$

This form is used because a value of zero for the suitability index for any one of the three components indicates a lack of habitat to maintain viable populations of American toads.

Once it has been fully developed, a habitat model for the American toad could be used to assess the effects of such activities as road building, housing construction, environmental pollution, landfill operations, clearing of deciduous forests, draining or dredging of ponds and wetlands, intensive recreational use of wetlands, floodplains and the shoreline areas of lakes, and large changes in water level by removing or introducing water.

Habitat Models and Endangered Species Protection

The Wyoming toad (*Bufo hemiophrys baxteri*) has recently been listed as endangered by the U.S. Fish and Wildlife Service (Baxter et al. 1982). As of June 1988, there was only one small breeding population known to exist. There are no habitat models available for this subspecies and there have been few studies of its natural history. This is unfortunate because there is an urgent need to begin a recovery program. Information about the related Manitoba toad (*Bufo hemiophrys*) which has been more extensively studied could be used to infer habitat relationships, but this is obviously not as valid as studying the Wyoming toad directly. This situation illustrates why it is important to intensify our efforts to develop databases and habitat models for all species before they reach the point of becoming endangered. It also exemplifies the role a habitat model can play in identifying information gaps and focusing research efforts.

Discussion

Resource assessments require the development of models for the quantitative assessment of habitat suitability. It is essential that such models be developed in combination with comprehensive databases. A long range goal should be to develop databases with efficient retrieval systems so that it is possible to access all of the site-specific natural history information available in the literature, and in the files of researchers and resource managers. The databases should also be constructed so that information gaps and priority areas for research can be identified.

This paper has emphasized producing habitat models for individual species as if these species exist in isolation. Hutto et al. (1987) have criticized the overemphasis on species

approaches in conservation programs as too narrow and they point out that we must not lose sight of the higher order patterns and processes which occur among interacting species. They suggest supplementing the species approach with approaches that consider such things as landscape patterns that maintain ecosystem level processes, the use of geographic information systems, and other land-based approaches.

Studies emphasizing the role of anurans in ecosystems should result in a better understanding of ecological process occurring at the terrestrial-aquatic interface, and could also contribute to more effective management of species which depend on these edge habitats and ecotones.

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Preliminary Report on Effect of Bullfrogs on Wetland Herpetofaunas in Southeastern Arizona¹

Cecil R. Schwalbe and Philip C. Rosen²

The bullfrog (*Rana catesbeiana*) is North America's largest frog and one of the most widely distributed anurans on the continent. Occurring naturally from Florida to Nova Scotia and west into central Texas, Oklahoma, and Kansas, the bullfrog has been introduced widely into permanent waters throughout the West (Bury and Whelan 1984, Stebbins 1985, Wright and Wright 1949). Known to be voracious, opportunistic predators, they have been implicated in declines of native anuran populations (Bury and Luckenbach 1976, Bury et al. 1980, Conant 1975, 1977, Jameson 1956, Moyle 1973, Nussbaum et al. 1983, Vitt and Ohmart 1978 and others). Much less is known about their impacts on other vertebrate classes.

A recent investigation of factors producing decline of Mexican garter snakes (*Thamnophis eques*) in Arizona (Rosen and Schwalbe 1988) suggested that predation by introduced bullfrogs (see fig. 1) is a present and

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Abstract.—Ranid frogs (*Rana catesbeiana*, *R. chiricahuensis*, and *R. yavapaiensis*), garter snakes (*Thamnophis eques*, *T. marci*) and Sonoran mud turtles (*Kinosternon sonoriense*) were surveyed in southeastern Arizona. Distribution of the introduced bullfrog (*Rana catesbeiana*) was negatively correlated with distributions of the two leopard frogs and garter snakes. The hypothesis that bullfrog predation caused decline of a native wetland herpetofauna is supported by data on bullfrog diet, on garter snake, leopard frog and mud turtle population structure, and natural history observations on the snakes. An experimental removal of bullfrogs has been initiated at the San Bernardino National Wildlife Refuge.

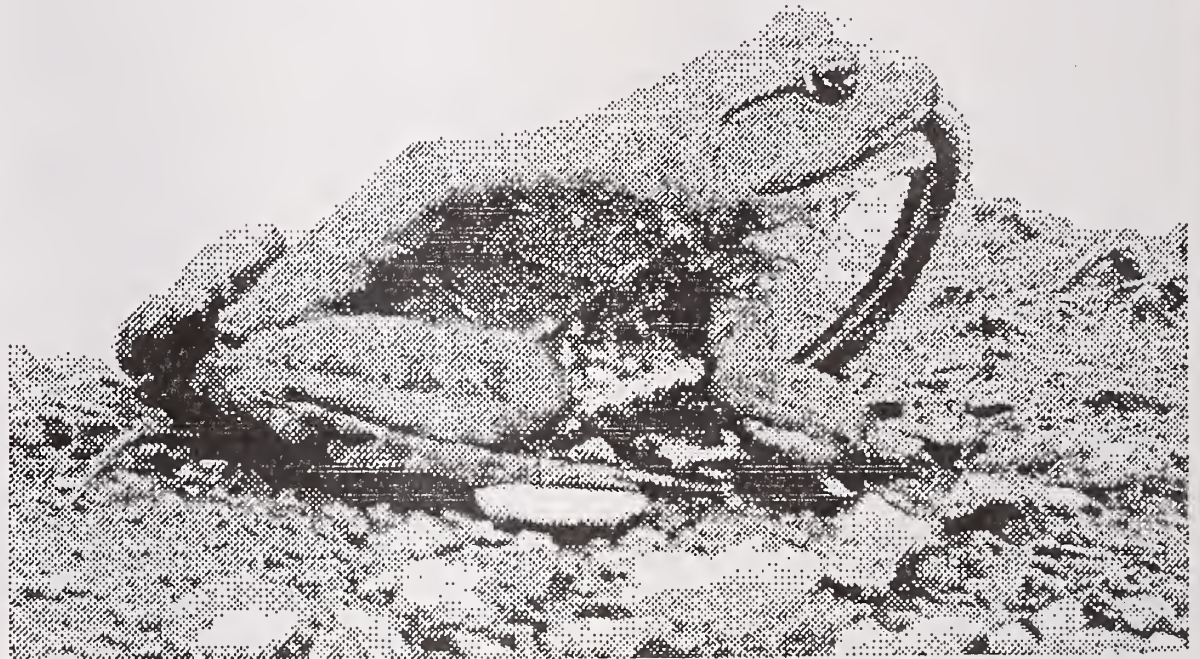


Figure 1.—Bullfrog swallowing adult or subadult Mexican garter snake, Parker Canyon Lake, Cochise Co., Arizona, 1964. Photo courtesy of John Carr.

serious impact on some of the few remaining snake populations. Observations during the garter snake survey suggested a similar effect on leopard frogs (*Rana yavapaiensis*, *R. chiricahuensis*).

Recently, Hayes and Jennings (1986) questioned the importance of bullfrog predation in declines of western North American ranid frogs. They include predation by bullfrogs as one of three major hypotheses to explain decline of ranid frogs in California, but suggest that predation by introduced fish has had greater im-

act on native frogs. Hayes and Jennings (1986) indicate further that their hypotheses need to be tested to determine actual causal factors in population declines. In this paper we present distributional and natural historical data implicating bullfrogs in population declines of native wetland reptiles and amphibians in southeastern Arizona. We then describe an experimental program of bullfrog removal we have initiated to test the direct and indirect effects of this introduced predator on wetland herpetofaunas.

Methods and Materials

We report on two phases of our work. The first phase involves extensive surveys, principally for garter snakes. The second focuses on intensive surveying and experimental manipulation at one locality that is heavily infested with bullfrogs.

Extensive Phase

We sampled over 80 localities throughout much of central and southern Arizona during 1985-1987, searching appropriate aquatic and semi-aquatic habitats (Rosen and Schwalbe 1988). Methods and results are briefly summarized here. Lotic habitats were surveyed for 2-6 mile reaches on foot. Lentic habitats were also examined on foot, in their entirety in most cases. During these

surveys, attempts were made to capture, measure, mark and release all garter snakes seen. Detailed observations were made on distribution and abundance of other biota on the sites sampled, with special attention to anurans, turtles and other snakes. Intensive mark-recapture studies were conducted at four sites using trapping methods described below.

Intensive Phase

San Bernardino National Wildlife Refuge (SBNWR), one of four sites where mark-recapture procedures were initiated during the extensive phase of our work, was selected for ongoing observation and experimentation. Beginning in September 1986, we visited the refuge in September and May of each year, marking snakes, observing herpetofaunal dis-

tributions and abundances, and experimentally removing bullfrogs.

Intensive Site Description

SBNWR (fig. 2) consists of 984 ha in the San Bernardino Valley on the Mexican border in Cochise County, Arizona. Elevations range from 1134 to 1183 m. Higher, rocky slopes and mesas supporting Chihuahuan desertscrub and lower terraces grading into desert grassland comprise almost two-thirds of the refuge.

The heart of the refuge is a low-land supporting dense mesquite (*Prosopis velutina*) bosques and sacaton (*Sporobolus*) grasslands interspersed with four spring-fed ponds and seven additional springs. In the center of this low ground is deeply incised Black Draw, headwater of the Rio Yaqui, which normally arises at a natural spring about halfway between the Mexican border and north boundary of the refuge. Large, isolated, living and dead cottonwood trees (*Populus fremontii*) occur near almost all aquatic habitats. Broad swamplike cienegas with little open water occur at the artesian wells that do not supply ponds.

Vegetation in Black Draw varies from rank herbaceous plants and tall grass in the northern one-half, through open riparian thicket and cat-tail (*Typha domingensis*) stands, into almost impenetrable thickets of sapling cottonwood and willow (*Salix gooddingi*) throughout the lower 1.2 km to the border. Cienega pools are cold and reach a depth of about 2 meters.

North Pond, focal point for the experimental removal of bullfrogs, contains 0.1 ha of open water surrounded by earthen levees. Artesian well flow is piped into the pond and into a small marshy area north of the pond. North and west banks are lined with mesquite. South and west banks are open or overgrown with herbaceous vegetation. Cat-tail is spreading rapidly around the pond

SAN BERNARDINO NWR

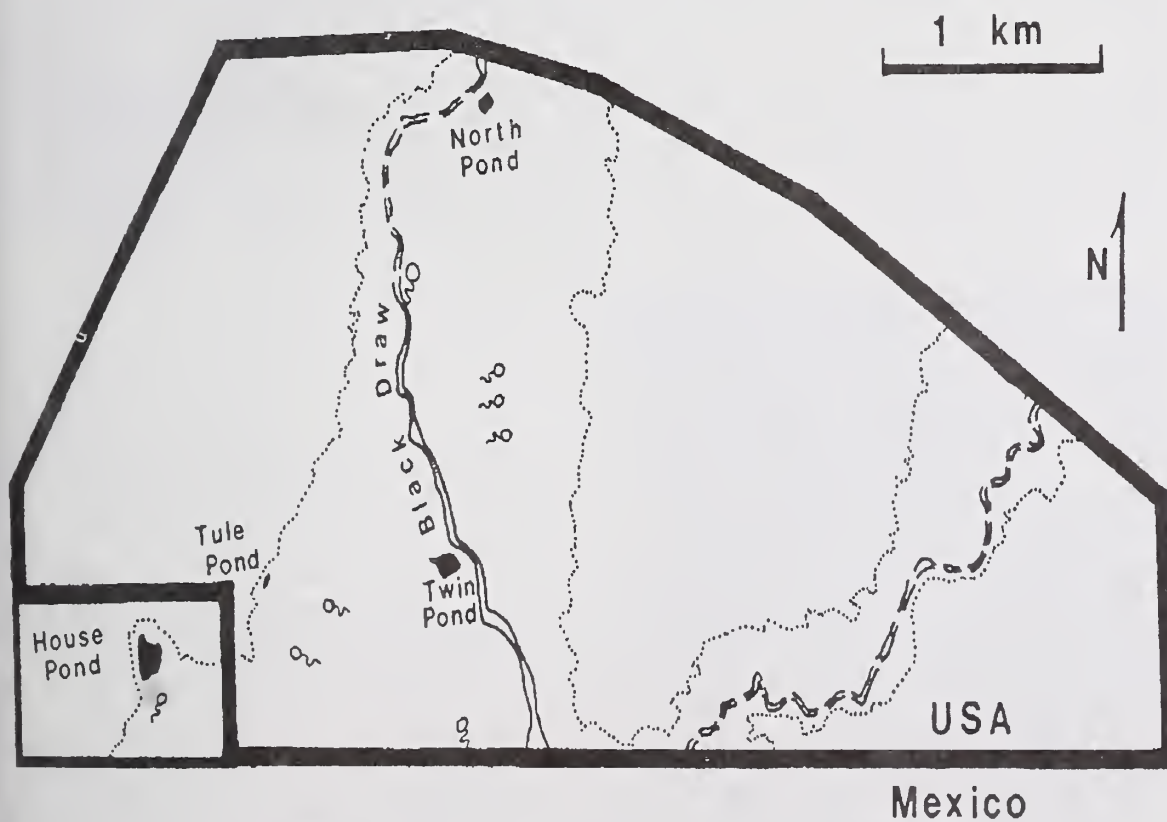


Figure 2.—Diagrammatic map of San Bernardino National Wildlife Refuge. Stippled line indicates boundary between upland Chihuahuan desertscrub and riparian scrub and woodland vegetation types.

margin from foci in northeast and southwest corners. Open water is largely choked with submergent macrophytes.

The wetland herpetofauna of the refuge includes bullfrogs (*Rana catesbeiana*), lowland leopard frogs (*R. yavapaiensis*), Mexican garter snakes (*Thamnophis eques*), checkered garter snakes (*T. marcianus*), and Sonoran mud turtles (*Kinosternon sonoriense*).

Intensive Field Procedures

Garter snakes were collected by hand at all times of day and night, and with minnow traps connected by aquatic drift fences (see Rosen and Schwalbe 1988 for details). Four drift fences, each with a trap at each end, were set in North Pond during each visit to the refuge. Two drift fences with traps were set in Twin Pond in August 1985 and August-September 1986. Twin Pond was drained during summer 1987 and remains dry.

The following data were recorded for each snake captured: date, location, sex, snout-vent length (SVL), tail length, total weight, presence/absence and number of food items, and injuries. Females were palpated to determine presence/absence and number of developing young. For hand-caught snakes we recorded activity at time of first sighting, microhabitat, time, and cloacal and ambient temperatures. Each individual was uniquely marked by clipping subcaudal scales.

Bullfrogs were collected mostly with four-pronged spears at night by using head lamps to find and blind them. Additionally, many were collected in turtle hoop nets, which were set along seine nets rigged as aquatic drift fences. Some hoop nets were baited to capture turtles, and these captured bullfrogs, as well. A few were collected by hand and with air guns and light arms. Initial collecting efforts were focused on larger

(≥ 100 mm SVL) bullfrogs. Every aquatic habitat on the refuge was checked for frogs by listening for their calls and searching visually at night. Captured bullfrogs were kept on ice overnight and the following data were recorded the next day: capture location and date, sex, snout-vent length, total weight. Most were dissected to determine stomach contents and reproductive condition.

Results

Distribution and Natural History

Leopard frogs are significantly less common where bullfrogs abound (table 1: Spearman rank correlation $r_s = -0.434$, $p < 0.025$, Rosner 1982, Sokal and Rohlf 1981). SBNWR is the only site where we found both bullfrogs

and leopard frogs. Among the sites shown in table 1, introduced, non-native predatory fish were found in abundance only at Bog Hole and Babocomari Cienega, where ranid frogs were absent. Historical records indicate that leopard frogs once were abundant in two areas now supporting dense bullfrog populations, Arivaca Creek (Wright and Wright 1949) and SBNWR (Lanning 1981, Lowe personal communication).

Mexican garter snakes also are significantly less abundant in the presence of bullfrogs (table 1: Spearman rank correlation $r_s = -0.420$, $p < 0.03$). At the Potrero Canyon locality, Mexican garter snakes were known as late as 1970 (Rosen and Schwalbe 1988), but we found only checkered garter snakes ($N = 24$) during 1985-1987.

At SBNWR, all museum records of *Thamnophis* prior to 1970 ($N=7$) were

Table 1.—Distribution and abundance of ranid frogs and garter snakes in wetlands of southeastern Arizona, based upon field work during 1985-1988. 0=absent, 1=rare, 2=common, 3=very abundant; P=pond, C=cienega, M=marsh; NWR=National Wildlife Refuge; SB=San Bernardino. Leopard frogs may be either *Rana chiricahuensis* or *R. yavapaiensis*.

Locality		Ranid abundance		Garter snake abundance	
		Bull-frog	Leopard frog	Checkered	Mexican
San Bernardino NWR	P	3	0	1	1
San Bernardino NWR	C	3	1	1	1
Upper SB valley	P	0	2	3	0
Leslie Creek	C	0	3	0	0
Lewis Springs	C	0	3	0	2
San Pedro River		2	0	2	1
San Pedro gravel pit	P	3	0	0	0
Ramsey Canyon	P	0	3	0	0
Parker Canyon Lake		3	0	0	1
Sharp Spring	C	1-2	0	0	1
Bog Hole	P	0	0	0	0
Bog Hole	C	0	0	0	3
Research Ranch	P	0	2	0	3
Research Ranch	C	0	1	0	3
Elgin Cienega	C	0	2	0	2
Babocomari River	P	0	0	0	1
Babocomari River	C	0	0	0	1
Cienega Creek	C	1	0	0	2
Potrero Canyon	M	3	0	3	0
Potrero Canyon	C	3	0	2	0
Sonoita Creek	M	3	0	0	0
Sonoita Creek	C	3	0	0	0

eques, while all subsequent (N=5) were *marcianus*. *Thamnophis eques* comprised 57% of the garter snakes seen on the refuge during 1985-1988 (table 2). On the refuge, the population of Mexican garter snakes was heavily dominated by large adults, in significant contrast to populations in areas lacking bullfrogs, where yearlings and small adults predominate (fig. 3, Mann-Whitney U Test, $p < 0.001$). At SBNWR, most Mexican garter snakes (61.9%) had damaged tails which bled between the ventral scales when handled (fig. 4), suggesting unsuccessful predation attempts by bullfrogs. This type of injury was not seen at any other locality.

At SBNWR we found Sonoran mud turtles (*Kinosternon sonoriense*) to be unexpectedly rare. Only four

turtles were captured in 29 trap-nights on the refuge, a rate of 0.14 captures per trap-night. Elsewhere in Arizona, 917 trap nights produced 2,092 captures at the 17 other localities we have sampled (Rosen unpublished data, Rosen 1987). The mean trap success for those 17 localities was 4.32 ± 0.23 captures per trap-night (range 0.20-12.23). For the five habitats in southeastern Arizona which were comparable to the refuge, and where at least 20 trap-nights were registered, mean trap success was 5.42 ± 1.03 captures per trap-night (1.23-12.23). Quitobaquito Pond, with 0.20 captures per trap-night was the only area in Arizona with trapping success approaching the low level obtained at the refuge. The Quitobaquito population is

known to have been markedly reduced by human activities (Rosen 1986).

Including captures obtained by all methods, only six Sonoran mud turtles have been found by us on the refuge. All were large adults, and, according to growth ring analysis (see Rosen 1987), all were born prior to 1981. In all other populations, juveniles comprised over 20% of the sample (Rosen, unpublished data).

Bullfrog Diet

Stomach contents confirmed the opportunistic feeding behavior of bullfrogs (table 3). Invertebrates constituted the majority of food items, with the snail, *Planorbella tenuis*, and insects of the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Odonata and Orthoptera commonly eaten. Arthropods consumed included adults and larvae of terrestrial, aquatic and flying forms.

Vertebrates were found in 14.6 percent of the stomachs that contained some food. The most commonly consumed vertebrates were other frogs, including bullfrogs. At least two species of native fishes, both endangered, were eaten, the Yaqui chub (*Gila purpurea*) and the Yaqui topminnow (*Poeciliopsis occidentalis sonoriensis*). Mammal prey included *Peromyscus*, a *Sigmodon* and other as yet unidentified small rodents. The two reptile food items were a neonate checkered garter snake in a frog from House Pond and a spiny lizard (genus *Sceloporus*). Not shown in table 3 was a nestling bird, thought to be a red-winged blackbird, *Agelaius tricolor*, found in the stomach of a subadult bullfrog (100 mm SVL).

Bullfrog Density

Using the numbers of bullfrogs removed from North Pond (table 4), we can estimate density and bio-

Table 2.—Records of all garter snakes captured on the San Bernardino National Wildlife Refuge, Arizona, 1985-1988.

Sampling period	Number Mexican garter snakes	Number checkered garter snakes	Snakes captured per day
16-18 Aug 85	3	2	1.67
23-27 May 86	4	3	1.40
30 Aug-1 Sep 86	3	1	1.33
23-25 May 87	5	0	1.67
5-7 Sep 87	4	6	3.33
29-30 May 88	1	3	2.00
Total	20	15	1.84

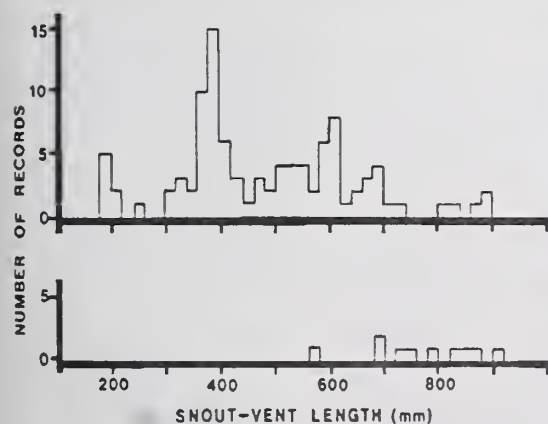


Figure 3.—Size-frequency histograms of Mexican garter snakes in 1985 and 1986 (modified from Rosen and Schwalbe 1988). Upper histogram represents snakes from populations where bullfrogs were scarce or absent. Lower histogram represents San Bernardino National Wildlife Refuge sample.

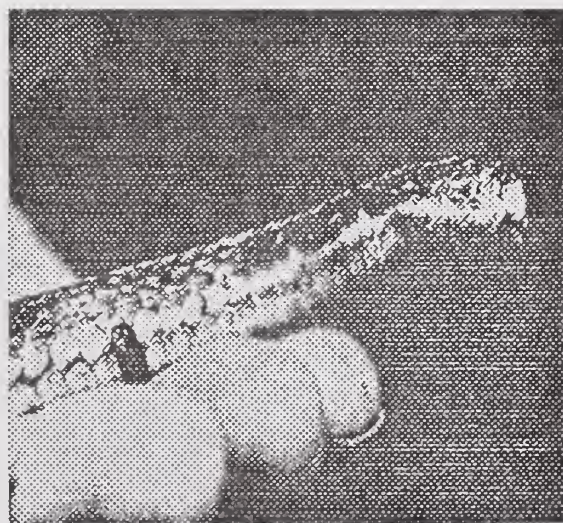


Figure 4.—Bullfrog damage to tail of large Mexican garter snake, San Bernardino National Wildlife Refuge, Cochise County, Arizona, 1986.

mass. After removing 74 adult bullfrogs in spring 1987, we estimated 5 adults remained. Including the small area of marsh north of the levee, there was 0.11 ha of habitat for this population, giving a minimum density estimate of 718 adults/ha. Mean weight for all frogs removed in the spring 1987 census at North Pond was 217.1 g, yielding a total biomass of 23.7 kg, or 215.5 kg/ha. Excluded from this biomass estimate were remaining adults, and numerous juveniles that were not hunted. These estimates are conservative since we had already removed 51 adults and 23 juveniles during fall 1986, before we had determined the most effective means of removing the frogs.

The fall 1987 census at North Pond reflects thorough removal the previous spring, with only about 10 frogs either maturing into adults or immigrating between May 24 and September 5, 1987. We estimated that 4-6 adults remained in North Pond at the end of our 1987 collecting. Because of extremely cool, windy weather during the spring 1988 trip, we were unable to collect bullfrogs effectively during the last night and left an estimated 15-20 adults.

A total of 552 bullfrogs has been removed from SBNWR as of June 1988 (tables 4-5), including 358 of adult size, from a total area of 2.4 ha of open water. We estimate that take to represent 55-80% of the adult bullfrogs on the refuge at that time.

Preliminary Experimental Results

Leopard frogs bred successfully at the spring source in central Black Draw in early 1987, a time of unusually good rainfall. This area was virtually devoid of bullfrogs because it is open enough for predators and resource managers to kill all or almost all adults. In May 1987, leopard frog tadpoles and juveniles were moderately abundant from the spring to the northernmost reach of cienega-stream and dense sapling thicket,

where they were replaced by bullfrogs. The first confirmation of leopard frogs in North Pond was five found in bullfrog stomachs in May 1987. No noticeable further increase in leopard frog numbers or distribution was observed in May 1988.

The first juvenile Mexican garter snake on the refuge during this study was recorded in fall 1987. The capture rate of garter snakes on the refuge doubled between May and September 1987 following bullfrog removal (table 2). Extremely cold,

windy weather on the May 1988 trip greatly depressed reptile activity. Thus, the 2.0 garter snakes captured per day (table 2) may reflect a decrease in activity rather than a decrease in the numbers of garter snakes on the refuge.

Discussion

Distributional and natural historical data from southeastern Arizona provide prima facie evidence that bull-

Table 3.—Stomach contents of adult (>120 mm snout-vent length) bullfrogs, San Bernardino National Wildlife Refuge, Arizona.

Prey type	Sampling date				Total
	30 Aug-1 Sep 86	5-6 Sep 87	22-24 May 87	29-30 May 88	
Amphibians					
Bullfrogs					4
Tadpoles	2	—	2	—	4
Juveniles	3	—	1	—	
Leopard frogs					5
Juveniles	—	—	5	—	
Unknown anurans	5	3	5	2	15
Fishes					3
Yaqui chub	2	—	—	1	
Yaqui topminnow	—	—	1	—	1
Unidentified	—	—	8	1	9
Mammals	2	—	2	1	5
Reptiles	—	—	1	1	2
Invertebrates	86	14	139	302	541
Detritus	7	4	29	17	57
Empty stomachs	10	7	24	7	48
Total food items	100	17	164	332	613
No. frogs dissected	55	15	117	65	252

Table 4.—Removals of bullfrogs from North Pond, San Bernardino National Wildlife Refuge, Arizona. Individuals >120 mm snout-vent length are considered to be adults.

Sampling period	Adult males	Adult females	Total juveniles	Total removed
Fall 1986	33	18	23	74
Spring 1987	43	31	35	109
Fall 1987	14	1	13	28
Spring 1988	17	15	48	80
Totals	107	65	119	291

frogs play a causative role in population decline and disappearance of native wetland amphibians and reptiles (table 1; Results). For Mexican garter snakes, this evidence is bolstered by data on population structure (fig. 3) and by observations of injuries caused by bullfrogs (fig. 4; Rosen and Schwalbe 1988).

That bullfrogs are predatory generalists has been thoroughly documented (see extensive review of bullfrog foods in Bury and Whelan 1984). In Arizona alone, bullfrogs have consumed such vertebrate prey as a nestling bird, young muskrat (*Onychomys leucogaster*), cotton rat (*Sigmodon*), softshell turtle (*Trionyx spiniferus*), spiny lizard (*Sceloporus*), kingsnake (*Lampropeltis getulus*), several species of fish and frogs, garter snakes, even a rattlesnake (*Crotalus atrox*) (fig. 1, table 3; Clarkson and deVos 1986).

To our knowledge, in southeastern Arizona, the only place where bullfrogs abound and where leopard frogs and Mexican garter snakes also still occur, albeit rarely, is SBNWR. We believe the native species persist there because the extent and diversity of aquatic habitats is greater than elsewhere in the region. Specifically, the relatively sparse vegetation and absence of deep pools at the spring source area in central Black Draw has remained largely free of adult bullfrogs. This is where leopard frogs

have bred and where the smallest Mexican garter snakes have been found.

We believe the reason only five leopard frogs and one garter snake were found in bullfrog stomachs is due to already severe reduction of leopard frog and garter snake populations. The same reasoning may apply to the absence of hatchling Sonoran mud turtles in bullfrog stomachs.

The bullfrog density at North Pond (SBNWR) was quite high for Arizona populations, although not necessarily high for other parts of its range (Currie and Bellis 1969). Such a density is equalled and possibly exceeded at Arivaca, Pima County, Arizona, where both leopard frogs and Mexican garter snakes have been extirpated or become extremely rare (Rosen and Schwalbe 1988). Concentrations of bullfrogs similar to that in lower Black Draw have only been seen in comparable habitat in portions of one cienega in the San Raphael grasslands of Santa Cruz County. Abundances comparable to those in House Pond occur at a gravel mine south of Arizona Highway 90 on the San Pedro River, Cochise County; at Page Springs, Yavapai County; and possibly at Parker Canyon Lake, Cochise and Santa Cruz counties and Potrero Canyon marsh, eight kilometers north of Nogales, Santa Cruz County.

At Potrero Canyon marsh, Mexican garter snakes have disappeared and checkered garter snakes are abundant. In the preceding three localities, checkered garter snakes are absent, and Mexican garter snakes persist in low numbers. Both garter snakes occur along the San Pedro River but neither utilize the gravel pit pond (Rosen and Schwalbe 1988, Rosen personal observations).

Natural cienega-streams, including Turkey and O'Donnell Creeks, where bullfrogs are absent, and Cienega Creek, where they are rare, have high densities of Mexican garter snakes and include many juveniles and young adults. One spring fed pond north of Canelo Hills, which is structurally and vegetatively similar to North Pond, contained about 95 Mexican garter snakes at a density near 1055 individuals/ha, and yielded an average of 5.4 snakes per trapping day (Rosen and Schwalbe 1988). In contrast, only seven garter snakes have been trapped on SBNWR in fifteen days of similar trapping.

Central Black Draw would ordinarily be regarded as relatively poor habitat for Mexican garter snakes, because the vegetative cover is too thin, particularly at the water's edge. The abundance of Mexican garter snakes there and the regular occurrence of checkered garter snakes at North Pond display an inversion of the usual habitat preferences of the two species in Arizona. In competition, in a broad sense, with Mexican garter snakes, checkered garter snakes may be favored by the presence of bullfrogs because they are less aquatic and hence less affected by the increased predation pressure.

Hayes and Jennings (1986) argued that predation by introduced bullfrogs was not a compelling hypothesis to explain population declines of native ranid frogs in western North America. They suggest that predation by introduced fish, mainly centrarchids, is a more promising hypothesis. In southeastern Arizona we

Table 5.—Bullfrog removals from aquatic habitats other than North Pond, San Bernardino National Wildlife Refuge, Arizona. Individuals > 120 mm snout-vent length are considered adults.

Locality	Date	Adult males	Adult females	Juveniles	Total removed
Twin Pond	Fall 86	2	2	1	5
Tule Pond	Spring 87	2	3	3	8
House Pond	Spring 87	35	42	34	111
Black Draw	Spring 87	32	25	15	72
Tule Pond	Spring 88	0	0	3	3
House Pond	Spring 88	9	10	11	30
Black Draw	Spring 88	6	18	8	32
Totals		86	100	75	261

found that bullfrogs have invaded a greater variety of wetland environments than exotic predatory fish, and, in some instances, have achieved population densities sufficient to impact the native herpetofauna. While we do suspect that introduced fish impact native wetland herpetofaunas in Arizona (see Rosen and Schwalbe 1988), our data for the southeastern portion of the state compellingly incriminate the bullfrog.

Our approach is to attempt to manage or eliminate bullfrogs from selected areas. It is principally intended to develop practical management techniques for controlling bullfrogs, but should also provide an experimental test of the bullfrog predation hypothesis.

Effective January 1, 1988, the Arizona Game and Fish Commission opened the season year round and set an unlimited bag and possession limit on dead bullfrogs statewide except for La Paz, Mohave, and Yuma counties (Arizona Game and Fish Commission 1988). The stipulation of unlimited possession of dead frogs was to decrease the likelihood of accidental or intentional release of bullfrogs into new habitats. The new regulations will make it easier for agencies, organizations and individuals to put pressure on bullfrog populations in specific areas in favor of native species.

No data exist to show impacts of bullfrogs on native species in the three western counties, so they have retained a July 1 to November 30 season with a bag and possession limit of 12 per day or in possession live or dead. Because Arizona's amphibian and reptile regulations are reviewed annually, new data can be incorporated into management decisions.

Conclusions

There is evidence that bullfrogs have negatively impacted populations of native amphibians and reptiles in

Arizona. Although some of the trends are encouraging, preliminary data from bullfrog removal experiments are inconclusive as to whether or not bullfrog control measures may augment recruitment in lowland leopard frogs, Mexican garter snakes or Sonoran mud turtles. More intensive efforts will be required to eliminate bullfrogs from even local habitats when such habitats are structurally complex.

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Developing Management Guidelines for Snapping Turtles¹

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In general, turtles have not been a major concern of wildlife managers in North America, and in many jurisdictions they are given little or no protection. They are perceived to have limited ecological, commercial, aesthetic or recreational value, and because they are usually cryptic and slow moving they are uninteresting to most people. Partly for these reasons, there have been remarkably few studies of their life history and ecology. In addition, their great longevity makes them difficult to study, except on a long-term basis. Nevertheless, turtles are, or should be, of interest to wildlife managers for at least three major reasons.

First, they are major components of a variety of both terrestrial and aquatic ecosystems and therefore play significant, though often unrecognized roles as carnivores, herbivores and scavengers. In both aquatic and terrestrial habitats, the

standing-crop biomass of turtles is generally much higher than that of any other reptile (Iverson 1982). In aquatic systems, turtle biomass often exceeds that of sympatric endotherms by an order of magnitude and is similar to levels reported for fishes (Iverson 1982). Similarly, annual production of turtles is comparable to that reported in most other vertebrates, although well below levels found in some fishes (Iverson 1982). Many turtles that are especially long-lived may have low annual productivity. This low productivity may be overestimated because of the high standing-crop biomass of turtles. Their life history is markedly different from those of the birds and mammals that typically occupy the attention of wildlife managers. As such, these species represent special problems in conservation and management. Therefore, turtles should be of interest to managers, because they are important components of a variety of ecological communities and because in many cases their longevity and low annual production relative to standing crop, characteristic of a "bet-hedger" (Obbard 1983) is a life-history strategy that may be highly susceptible to exploitation or to other sources of mortality of adult animals such as unsuitable overwintering conditions or heavily polluted waters.

Secondly, managers should have an interest in turtles because many species are harvested for commercial

profit, usually as food or for the pet trade (Bergmann 1983, Congdon et al. 1987, Lovisek 1982). There is evidence of marked, recent declines in harvests of most turtle species, but this evidence is difficult to quantify because estimates of total stocks do not exist for any turtle species. For snapping turtles, the annual commercial catch in Minnesota was estimated at 36000-40800 kg or approximately 6000-6800 average-sized adults (Helwig and Hora 1983). In southern Ontario, Lovisek (1982) estimated the annual catch of *C. serpentina* to be 30000-50000 kg or 5000-8300 adults. There is evidence from trappers (J. Bullard pers. comm.) that numbers of this species are a fraction of former numbers over much of their southern range in Ontario, but again no quantitative estimates exist. At present, therefore, it is necessary to measure the impact of harvesting turtles on a local basis (Hogg 1975).

Thirdly, snapping turtles may be of interest to managers because they are often regarded as pests or as a danger to human swimmers, or as destructive predators of waterfowl and game fish (Hammer 1969, Kiviat 1980, Pell 1941).

In this paper, we review the biology of snapping turtles in relation to these three areas of potential importance for wildlife managers. We present demographic characteristics of 2 populations in Ontario, and in addition, we develop a life table for the more northern population of snap-

Abstract.—We examined demographic features of 2 Ontario populations of snapping turtles (*Chelydra serpentina*) to provide an empirical basis for developing management guidelines. The northern population matured later (18-20 yr) than did the southern populations (<10 yr), and displayed an older age distribution. Long-lived, "bet-hedging" species have low annual reproductive success and are unusually susceptible to exploitation. A preliminary life table is presented for the northern population. Our results indicate that the northern population cannot sustain even minimal levels of exploitation by humans without undergoing a decline in numbers.

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ping turtles which will allow us to predict the impact of different levels of harvesting pressure on this population.

Snapping Turtles in Aquatic Ecosystems

Regulation of Population Density

There is at present little understanding of what factors regulate populations of any turtle species, but it is known that turtles may reach very high densities and high biomass densities (Galbraith et al., in press; Iverson 1982). It seems likely that primary productivity would be the best predictor of variation in numbers of turtles in a habitat. In snapping turtles, population density ranges from 1-75 adult turtles per ha (Galbraith et al., in press). Density among populations correlates positively with latitude and primary production levels and negatively with the size of the body of water (Galbraith et al., in press), although data are too sparse to rely heavily on these correlations. Other possible factors influencing density are predation pressure, especially on nests and hatchlings, climatic influences on egg survival and embryo development, and availability of suitable nesting sites. Again, the role of these factors has not been studied.

Annual Energy Budgets

No complete energy budget has been determined for any turtle population, although some efforts have been made to estimate critical components of the energy budget (Congdon et al. 1982). Almost all efforts in this area have concentrated on the energy content and cost of the eggs (Congdon and Gibbons 1985, Congdon and Tinkle 1982, Shine 1980) and on the rates of digestion, especially in relation to temperature (Parmenter 1981).

Food-Web Connections

Snapping turtles are widely regarded as voracious predators, but most studies of their diet indicate that plant material is a major component of their food (Alexander 1943, Hammer 1972, Pell 1941). Hammer (1972) found that plants made up the majority of the diet of snapping turtles in a North Dakota marsh. In Connecticut, fish (mostly nongame species) and aquatic plants were of equal importance and birds made up only a small fraction of the diet (Alexander 1943). In Maine, snapping turtles ate significant numbers of ducklings in local areas where both turtles and waterfowl were common, but widespread control of turtles was not recommended (Coulter 1957). Lagler (1943), working in Michigan, concluded that snapping turtles had minimal impact on waterfowl and pan fish and subsisted primarily on plant material and invertebrates. In general then, snapping turtle predation on waterfowl or game and sport fish poses no serious problem to these valuable species except perhaps in local situations where numbers of turtles may be very high and the turtles have easy access to young waterfowl.

Adult snapping turtles are largely immune to predation other than by humans over most of their range. A wide diversity of predators prey on snapping turtle eggs (foxes, skunks, raccoons) and hatchlings (herons, large fish), and mortality is very high during these stages.

Rationale for the Development of Life Tables

The demography of populations of freshwater turtles under exploitation has not been extensively studied. Some reports have cited large catches being removed from specific locations with apparently little impact on remaining numbers in the short term (e.g. Hogg 1975) but no study has

followed an exploited population in detail for any length of time. It is necessary, therefore, to infer the effect of harvesting on populations using demographic parameters of unexploited populations under long-term study. This paper describes 2 snapping turtle populations in Ontario, Canada and presents a life table for one of these populations.

Study Areas

Lake Sasajewun, Algonquin Provincial Park, Ontario

The Ontario Ministry of Natural Resources Wildlife Research Area (W.R.A. 45°35' N, 78°30' W, mean annual temperature 4.4°C), is located in the central area of Algonquin Provincial Park, in a region of mixed forest last logged in the 1930s. The snapping turtles inhabiting the lakes and streams running through the W.R.A. have been studied since 1972. Each year, adult female turtles are captured after nesting and both males and females are captured using baited hoop traps. Of the approximately 185 tagged snapping turtles in the watershed of the North Mada-waska River, about 100 are recaptured each year. Approximately 70 nests of known females are located each year.

Snapping turtles are the largest aquatic vertebrate in the W.R.A., with the exception of beavers (*Castor canadensis*) and occasional river otters (*Lutra canadensis*). The only other species of turtle in this watershed is the midland painted turtle (*Chrysemys picta marginata*), present in very small numbers (< 10). The density of the W.R.A. snapping turtle population is approximately 1.5 adults/ha in lakes (Galbraith et al., in press). The study area and the snapping turtle population have been described extensively elsewhere (Galbraith and Brooks 1987; Galbraith et al. 1987, in press; Obbard 1983).

Royal Botanical Gardens, Hamilton, Ontario

The Royal Botanical Gardens (R.B.G.) consist of approximately 700 ha of woodlands and waterways within the metropolitan Hamilton area (43°17'N, 79°53'W; mean annual temperature 9.8°C). This study area and the snapping turtle population in the R.B.G. have been described previously (Galbraith et al., in press). We have captured, tagged, and released adult and juvenile snapping turtles in this watershed since 1984. In addition to snapping turtles, map turtles (*Malaclemys geographica*) and painted turtles are common aquatic chelonians in this system. The painted turtle is at least as common as the snapping turtle.

The turtles inhabit a highly productive, eutrophic waterway which is artificially enriched by effluent from a sewage treatment plant. West Pond (9.8 ha), where our trapping has taken place, also connects with heavily-polluted Hamilton Harbour. Despite the contaminants, this population exhibits one of the highest densities yet reported for this species, approximately 60-70 adults/ha (Galbraith et al., in press).

Methods and Results

Life Tables

Two approaches are commonly taken in preparing life tables. Static or vertical life tables are prepared by deriving mortality rates from the observed population age structure. Cohort-specific, or horizontal life tables are prepared by following a specific cohort and observing age-specific mortality rates throughout life (Deevey 1947). At present, only static life tables can be prepared for snapping turtle populations, because individual cohorts cannot be followed effectively in these animals which may have a maximum longevity of over a century (Galbraith and Brooks 1987).

Therefore, we will only consider static life tables.

Life-Table Parameters for Algonquin Park (W.R.A.)

Snapping turtles experience large fluctuations in annual reproductive success (Obbard 1983). In the W.R.A. population, for example, most years do not produce any emergent hatchlings (R.J. Brooks, unpubl. data) whereas occasional years may produce large numbers of hatchlings. This highly stochastic survivorship throws some doubt on the utility of static life tables, because age curves could be highly biased by errors due to irregular recruitment. Therefore, we will use an average mark-recapture survivorship rate (Galbraith and Brooks 1987) for all adult females for the construction of the life table.

Several critical pieces of information have never been obtained for any snapping turtle population. For example, no estimate of survivorship of hatchlings or juveniles has ever been published. A crude estimate of this rate can be obtained by assuming that the number of turtles recruited per year into the population is fairly represented by the average recruitment rate, and that the number of eggs being produced per year has not varied greatly between the years when recruits were initially produced (i.e. as eggs) and the present time. In the W.R.A. population, on average, one new nesting female is captured per year on nesting sites used by approximately 85 other females. The mean clutch size of 34 eggs once per year gives an annual egg production of 2890 eggs. Assuming half these eggs produce females, the net survivorship across all age classes (including eggs) until age at first nesting (approximately 19 yr, (Galbraith 1986)) is therefore $1/1445$ (0.000692).

In the W.R.A. population, Obbard (1983) observed a mean rate of emergence of hatchlings from eggs of

0.0635, averaged over 142 nests in 5 yr. Taking this into account, in addition to the adult recruitment rate of one mature female per year, the probability of mortality between hatching and maturity for females in this population is 99.17%. Average annual juvenile survivorship from this estimate is therefore 0.7541 from hatching to 19 yr (table 1).

High rates of statistical errors within age estimates of individual turtles (Galbraith 1986) make documentation of horizontal rates of age-specific changes in fecundity unreliable, and therefore we have constructed our life table using mean clutch size for all age classes. Net fecundity, however, is a function of both clutch size and clutch frequency. Obbard (1983) estimated that 72.1% of adult females, on average, lay a clutch each year in this population. Mean annual egg production is therefore 24.514 eggs per female (mean clutch size is 34 eggs). For the purposes of a life table, the female turtles are considered as producing only female offspring. It is also necessary, therefore, to consider the effects of biases in hatchling sex ratios. Snapping turtles experience environmental sex determination, whereby incubation temperature during the middle third of the incubation period determines offspring sex (Yntema 1976). Between 1981 and 1985, the mean hatchling sex ratio of naturally incubated nests in the W.R.A. was 66% female (R.J. Brooks, unpubl. data). Therefore, each female turtle, on average, produces 16.18 female-destined embryos per nesting season. Although snapping turtles are long-lived, the life table for female snapping turtles in the W.R.A. suggests that they do not reproduce enough to sustain the population (table 1).

Life-Table Parameters for the Royal Botanical Gardens (R.B.G.)

Although data are inadequate to construct a meaningful life table for

snapping turtles from the R.B.G., some population parameters are known. For example, females in the very large snapping turtle population in the R.B.G. appear to nest for the first time at 10 yr of age (R.J. Brooks, unpubl. data), and the mean clutch size in the R.B.G. population between

1985 and 1987 was 45 eggs. The rate of mortality in this population is likely higher than in the Algonquin population, because numerous dead turtles are found each year (C.A. Bishop, unpubl. data). Essential but currently unavailable information from the R.B.G. population includes

long-term estimates of emergence rates of hatchlings or of adult survivorship, annual nesting frequency, and primary sex ratio.

Life-Table Implications for Management Guidelines

Clearly, exploitation of a population similar to that in Algonquin Park would quickly reduce numbers below any chance of recovery by reproduction within that population. In formulating our life table for the W.R.A., we have had to make several assumptions. The most important concerns our estimate of the rate of survival of hatchlings and juveniles.

A comparison between the 2 populations indicates that the advantages in the R.B.G. population of having a larger clutch size than the more northern population and being able to initiate nesting almost 10 yr before the W.R.A. population may be tempered by overestimating adult survivorship in the R.B.G. population. Consequently, lifetime reproduction may not be as high as one might predict. These comparisons must be improved by direct observation of survival in the critical juvenile years, and by following individuals of known age throughout life, in a variety of populations.

Considerable variation in population characteristics exists between these 2 populations located about 280 km apart. Trapping guidelines applicable to the R.B.G. population may not be suitable to the population in the W.R.A. Regardless, neither could likely tolerate harvests of more than 10% of the adult population.

Management Practices to Increase Yields of Snapping Turtles

It is evident that unregulated harvesting of adult snapping turtles will rapidly decrease population sizes, because adult turtles are normally

Table 1.—Life table for female snapping turtles in Algonquin Park (W.R.A.), Ontario, Canada.

Year class	a_x^1	l_x^2	q_x^3	m_x^4	$m_x l_x$	$\Sigma m_x l_x^5$
0	1907.4	1.000	.0635			
1	121.120	.0635	.7541			
2	91.343	.0479	.7541			
3	68.886	.0361	.7541			
4	51.950	.0272	.7541			
5	39.178	.0205	.7541			
6	29.546	.0155	.7541			
7	22.282	.0117	.7541			
8	16.804	.0088	.7541			
9	12.673	.0066	.7541			
10	9.557	.0050	.7541			
11	7.208	.0038	.7541			
12	5.436	.0028	.7541			
13	4.099	.0021	.7541			
15	3.091	.0016	.7541			
16	2.331	.0012	.7541			
17	1.758	.0009	.7541			
18	1.326	.0007	.7541			
19	1.000	.000524	.9660	16.18	.00848	0.00848
20		.000506	.9660	16.18	.00819	0.0167
21		.000489	.9660	16.18	.00791	0.0246
22		.000472	.9660	16.18	.00764	0.0322
23		.000456	.9660	16.18	.00738	0.0396
24		.000441	.9660	16.18	.00714	0.0468
25		.000426	.9660	16.18	.00689	0.0536
30		.000358	.9660	16.18	.03107	0.0847
35		.000301	.9660	16.18	.02615	0.1109
40		.000253	.9660	16.18	.02199	0.1329
50		.000179	.9660	16.18	.03404	0.1633
60		.000127	.9660	16.18	.02409	0.1873
70		.000090	.9660	16.18	.01705	0.1990
80		.000064	.9660	16.18	.01209	0.2111
90		.000045	.9660	16.18	.00853	0.2196
100		.000032	.9660	16.18	.00730	0.2269

¹ a_x = numbers of individuals.

² l_x = probability of survival from year class 0 to year class x .

³ q_x = probability of survival from year class x to year class $x+1$.

⁴ m_x = net fecundity at year class x (female-destined embryos produced).

⁵ $\Sigma l_x m_x$ = sum of all reproduction from year class 0 to year class x , equals R_0 , total lifetime reproduction, when x is at its maximum.

subject to very low rates of mortality (Galbraith and Brooks 1987). Two strategies are possible to increase harvestable numbers of turtles.

First, practical experience with sea turtle farming has shown that large numbers of eggs can be incubated under artificial or protected conditions (Mrosovsky and Yntema 1980), although care must be taken to incubate the eggs at a selection of temperatures which will produce a balanced sex ratio. Similar propagation of snapping turtles should result in increased numbers of juveniles in populations where adult numbers are not density-dependent.

Secondly, enrichment of the environment could provide faster growth rates for these poikilotherms. Increases in available protein will probably result in an increase in growth rates of individuals and increases in adult carrying capacities (MacCulloch and Secoy 1983).

Organochloride Contaminants and Human Consumption

Long-lived bottom-dwellers can accumulate high levels of environmental toxins, and snapping turtles have been found to carry very high loads of PCBs of various forms (Bryan et al. 1987a). Several studies have considered the way in which PCBs accumulate and in which tissues, and snapping turtles are now being employed as biomonitors for organochlorides in some studies (C.A. Bishop et al., unpubl. data).

Bryan et al. (1987) demonstrated that local levels of pollutants markedly affected the levels of organochloride toxins in snapping turtle tissues. Tissue-specific accumulation of PCBs is not random in snapping turtles, but is a function of lipoprotein content of the tissue and the high lipoprotein solubility of the toxins. Especially high concentrations (as high as 1600 ppm PCB in turtles from polluted locations) are found in fat bodies, brain, and testes. However,

Bryan et al. (1987) indicated that toxic PCB congeners did not remain in the large fat reserves of female turtles, as some had suggested, but were passed on in bulk to the egg yolks.

It is necessary, therefore, to test tissue or egg samples to ensure that turtles being harvested for human consumption are not loaded to a dangerous degree with organochloride contaminants.

Management of Snapping Turtles as Predators

Several studies have considered the impact of snapping turtles on waterfowl populations (Alexander 1943, Hammer 1972, Lagler 1943). Highly-productive bodies of water present ideal habitat for waterfowl and for turtles.

Destroying turtle nesting locations may not reduce local populations of snapping turtles, because females may migrate several kilometers between their usual home range and their nesting sites (Obbard 1977). In addition, such habitat interference will remove nesting opportunities for other turtle species.

Reduction in numbers of adult snapping turtles through trapping will rapidly deplete isolated populations and should reduce risks to prey species. However, if turtles can emigrate into the management area, then the expected long-term effect of culling adults will not be realized because the population can increase from these new adult immigrants.

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Spatial Distribution of Desert Tortoises (*Gopherus agassizii*) at Twentynine Palms, California: Implications for Relocations¹

Ronald J. Baxter²

The desert tortoise (*Gopherus agassizii*) is a species whose future is uncertain. Increased use of the deserts by man (Luckenbach 1982) has led to the point where the tortoise was officially listed as "threatened" in the state of Utah (Dodd 1980). The U.S. Fish and Wildlife Service stated in 1985 that "...listing [of the desert tortoise as a threatened or endangered species] is warranted but precluded by other pending proposals of higher priority" (Federal Register. 50(234): 49868-49870, 1985).

In California, the desert tortoise is the official state reptile, and is fully protected under law. The tortoise is also protected in Arizona and Nevada.

As part of a larger population study (Stewart and Baxter 1987) at the Twentynine Palms Marine Corps Air Ground Combat Center (MCAGCC), the spatial distributions of tortoise captures and burrows were analyzed and compared against randomly generated distributions. Questions asked were: (1) Are tortoise captures and burrows randomly located across the landscape

and/or are they associated with certain habitat types or site characteristics, and if so, (2) what implications do these distributions have for future management decisions?

Methods

Twentynine Palms MCAGCC is located approximately 5 kilometers north of Twentynine Palms, San Bernardino County, California, in the southwestern extreme of the Mojave Desert. All fieldwork was performed in the Sand Hill Training Area which is in the southwest corner of the MCAGCC. Elevations ranged from 865 meters atop Sand Hill to about 730 meters in the bottom of Surprise Springs wash. Data were collected Monday through Friday, 14 April through 18 July, 1986.

Systematic searching methods for tortoises and tortoise burrows were a derivation of procedures described by Berry (1984). A 1.29 square kilometer permanent study plot was established, with its approximate center being the NE 1/4, SW 1/4, NE 1/4, of S7, T2N, R7E (San Bernardino Base Meridian). This site offered a wide variety of habitats including washes, sandy basins, rolling hills and alluvial bajadas. The plot was divided into 64 equal sized "grids" of 142 meters on a side, with grid corners marked by posts. Grids were searched in parallel belts until the entire plot had been searched twice;

Abstract.—The spatial distribution of desert tortoises in relation to plant communities was compared against randomness. Tortoise captures ($n = 120$) and tortoise burrows ($n = 160$) exhibited non-random distributions across a 1.29 square kilometer study plot at Twentynine Palms, California. Results imply high diversity plant ecotones and communities, and possibly soil characteristics are important in determining tortoise densities. Non-randomness in tortoise populations dictates that relocation sites must include specific vegetational, topographic and edaphic habitats used by the parental populations.

once with the belts running north-south, and once with the belts running east-west. The plot was also randomly searched.

When an active tortoise was encountered, it was marked, weighed, sexed, measured and photographed. Each tortoise was assigned a unique number, and marginal scutes were notched with a small triangular file for relatively permanent identification. The precise location of the capture was noted by its distance (measured by rangefinder) and compass aspect to the nearest grid post. Data collected at each capture site included plant community, temperatures at the ground, 1 centimeter, and 1 meter, cloud cover, wind speed and direction, closest burrow, closest plant, and any unusual behavior.

Precise location of tortoise burrows were similarly determined by rangefinder and compass. Data collected at each burrow included plant community, distance and identification of nearest ecotone, distance to nearest wash, distance to nearest *Hilaria rigida*, slope aspect and steepness, opening compass aspect and position, length, depth, and tunnel characteristics. In this study area, it was difficult to determine if a burrow high on a slope above a wash was part of the wash "system." Therefore, it was arbitrarily decided to include burrows in the wash plant community only if they were actually found the wash bed.

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Six visually identified plant communities (Latr/Amdu, Hiri/Amdu, Mixed, Wash, Sparse Wash and Meadow) were mapped within the study plot, and seven 15-meter line transects (total of 105 meters) were measured which included bare ground as a species. Transects were

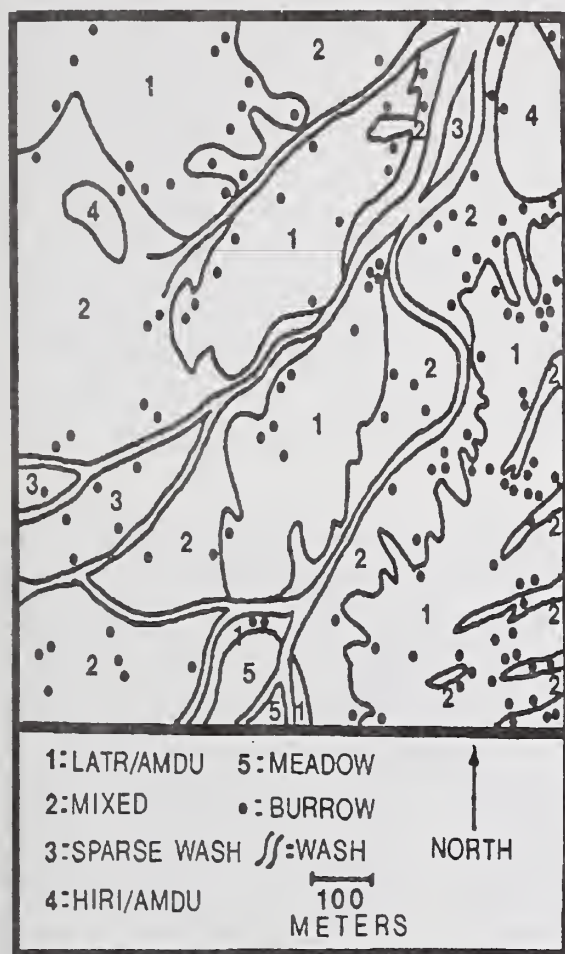


Figure 1.—Approximate distribution of plant communities and tortoise burrows across the study plot. See text for explanation of plant community names.

randomly located in each of these six communities. Standard transect statistics (density, coverage, frequency, relative density, relative coverage, relative frequency and importance values; Brower and Zar 1984) were computed for each community. Simpson's diversity indices (Simpson 1949) were computed and compared with Student's t-tests (Keefe and Bergerson 1977). Available annuals as well as perennials were used to give the best estimate possible for diversity. In addition, seven soil samples were taken in each community, and analyzed for soil separates (Brower and Zar 1984) and soil calcium (Hach 1983). Finally, nine "sand scats" were collected during the field work and tested for calcium.

A random model for capture and burrow locations was formed by combining a number of statistical tests. First a master map of the plot was constructed from actual field data at a scale of 1:2000. All capture positions, burrows and plant community boundaries were plotted on this map and checked against aerial photographs. The area covered by each plant community was then determined by the use of a planimeter. An X-Y scale ranging from 0 to 8 was plotted on the sides of the map, and a list of 328 random numbers was generated by computer. These numbers were paired, and the pairs be-

came the X-Y coordinates of random positions against which observed capture and burrow locations were compared. Distances to the nearest wash and ecotone were determined for these random locations by measuring them on the map, and compared against observed by Student's t-tests (Zar 1974). Observed capture distances were sometimes combined with previous data recorded in this area (Baxter and Stewart 1986).

A lack of habitat preference may be suggested if burrows and captures were found in the same relative abundance as the plant communities. In addition, if the expected plant abundance distribution differed significantly from random an extrapolation of observed distributional characteristics could be accomplished. An assumption of this test was that a distribution of randomly generated locations (with randomness confirmed) produced a random frequency distribution. Expected frequencies for burrows and captures were generated by multiplying the total number of actual burrows or captures by the percent of the plot encompassed by each plant community. These values were compared by a goodness-of-fit chi-square test (Zar 1974). In addition, the number of burrows or captures per grid were compared against expected values as derived from the Poisson distribution by a goodness-of-fit test.

Table 1.—Summary of plant community data from plant transects (total transect length = 105 meters).

Plant community ^a	No. of species	No. of individuals	Simpson's diversity index	Percent of plot area
Sparse Wash	16	733	0.6069	5.6
Hiri/Amdu	8	501	0.6841	4.0
Mixed	12	349	0.7247	37.2
Latr/Amdu	11	306	0.7688	50.6
Wash	25	292	0.7914	0.2
Meadow	15	662	0.7497	1.7
Bare Areas				0.7

^aSee text for explanation of community names.

Results

Plant Communities and Soils

Vegetation analyses revealed six distinct plant assemblages (table 1; fig. 1). Plant community distributions generally reflected the relief of the plot. The higher, more well-drained hills were dominated by an association of *Larrea tridentata* and *Ambrosia dumosa*, which encompassed plot area the most ("Latr/Amdu"; table 1) and exhibited relatively high plant diversity.

Found on 37.2% of the plot area was the "mixed" community that generally occupied intermediate areas between the Latr/Amdu and either washes or areas of high *Hilaria rigida* density. It was characterized by the association of *L. tridentata*, *A. dumosa* and *H. rigida*, and was found most often on the slopes above, and narrow linings next to washes. The edge, or ecotone, of this community with the Latr/Amdu community is extensively discussed below.

A highly diverse plant community was found in the washes (table 1; appendix 1). Such areas not only contained these perennial species, but also a significant number of other species found only in this community, giving it the highest species richness of any community.

Small uplifts within wash channels seemed to support a more open type of wash vegetation, "sparse wash." Such areas had many species common to the washes (appendix 1), yet much of this community was essentially pure stands of the opportunistic grass, *Schismus barbatus*.

A community ("Hiri/Amdu") consisting primarily of *H. rigida* and *A. dumosa* was located in upland basins where *L. tridentata* was not found. Such areas were low in habit and diversity, and very sandy.

Finally, near the south boundary of the plot, a small "meadow" of mostly *Baileya multiradiata* was found. Since no tortoises or tortoise burrows were found there, it was eliminated from further analyses.

Bare ground, when treated as a species in transect analyses, had overriding importance values and dominance in all communities (appendix 1). This is often the case in desert environments. Likewise importance values of *S. barbatus* were extremely high in all communities, pointing to the generally disturbed nature of the site. Comparisons of Simpson indices for the communities revealed significant differences ($p < 0.05$) in diversity for all communities except two. The Latr/Amdu and

wash communities were not significantly different ($p > 0.50$) in their diversity.

Soils were found to be somewhat similar in constituency (table 2), each

being composed to a large degree of sand. Soil calcium levels (table 3) were shown to differ significantly. No detectable calcium was found in any of the sand scats tested.

Table 2.—Summary of percent soil separates for plant communities.

Plant community ^a	Sand	Silt (%)	Clay	Classification
Sparse mixed	87	2	11	loamy sand
Hiri/Amdu	90	8	2	sand
Mixed	85	12	3	loamy sand
Latr/Amdu	70	20	10	sandy loam
Wash	81	3	16	sandy loam
Meadow	63	3	33	sandy clay loam

^aSee text for explanation of community names.

Table 3.—Summary of soil calcium levels and their significance.

Plant community ^a	Mean soil calcium (meq/100 mg soil)	Significantly different from	p ^b
Latr/Amdu	6.43	Hiri/Amdu	<0.006
		Wash	<0.05
		Mixed	NS
Hiri/Amdu	3.00	Wash	NS
		Mixed	<0.05
Mixed	1.48	Wash	NS
Wash	0.57		

^aSee text for explanation of community names.

^b2-sample t-test; corrected for type I errors; NS = not significant.

Table 4.—Distributions and significance of tortoise burrows per grid (Poisson, $n = 64$).

Number of burrows/grid	Number of grids random	Number of grids observed	Expected values random ^a	observed ^b
0	6	6	4.95	5.52
1	11	17	12.67	13.53
2	15	11	16.21	16.58
3	15	14	13.83	13.54
4	10	8	8.85	8.29
5 or more	7	8	4.67	6.30

^a $P > 0.98$

^b $P > 0.75$

Table 5.—Summary of frequency of tortoise burrows compared to plant community abundance.

	Plant community ^a					
	Sparse Wash	Hiri/Amdu	Mixed	Latr/Amdu	Wash	Other
% of plot	5.6	4.0	37.2	50.6	0.2	2.4
Random ^b						
observed	14	6	55	76	8	5
expected	9.2	6.6	61.0	83.0	0.3	3.9
Observed ^c						
observed	11	2	68	75	1	1
expected	8.8	6.3	58.8	80.0	0.3	3.8

^aSee text for explanation of community names.

^b $P < 0.001$, $n = 164$.

^c $P > 0.25$, $n = 158$.

Table 6.—Comparison of distance to washes between observed and random tortoise burrows.

Plant community ^a	Mean distance (m (SEM))		t	Degrees of freedom	P
	random	observed			
All communities	96.83 (6.80)	101.21 (7.83)	0.424	318	> 0.50
Mixed	79.54 (9.75)	68.66 (8.90)	0.821	120	> 0.50
Latr/Amdu	132.05 (10.07)	145.40 (12.17)	0.845	148	> 0.50

^aSee text for explanation of community names.

Table 7.—Comparison of distances to ecotone between observed and random tortoise burrows.

Plant community ^a	Mean distance (m (SEM))		t	Degrees of freedom	P
	random	observed			
All	96.83	101.21	0.424	318	> 0.50
Latr/Amdu	33.63 (2.65)	15.21 (1.80)	5.360	137	< 0.0005
Mixed	38.33 (9.09)	12.18 (1.60)	3.650	65	< 0.0005
Combined	34.05 (3.00)	13.99 (1.26)	6.493	203	< 0.0005

^aSee text for explanation of community names.

Tortoise Burrows

A total of 164 tortoise burrows was found on the study plot (fig. 1). Seventy-five percent were found under bushes, 14% with the opening under a bush but the tunnel proceeding into an open area, 8% with entrances in the open but the tunnels proceeding under a bush, and 3% entirely in an open area. Thus, almost all of burrows (97%) were associated with shrubs. Of these, 71% were associated with *L. tridentata*, 13% each with *H. rigida* and *A. dumosa*, and another 3% with other species.

Neither the distribution of observed or random burrows differed significantly from the Poisson expected frequencies (table 4). Likewise, when the distribution of observed burrows was compared against the distribution of random burrows, no significant difference was found (chi-square = 2.224; DF = 5; $p > 0.50$). Thus, when the entire plot area is considered, tortoise burrows exhibited a random pattern across the landscape. However, this was a relatively large scale test of burrows per arbitrary unit area, and says nothing about the pattern of tortoise burrows in relation to plant communities.

The abundances of tortoise burrows (both observed and random) in each plant community were compared against expected frequencies generated by the abundances of the plant communities (table 5). Burrows were sparse in the Hiri/Amdu and wash communities. Observed burrow frequency distribution did not differ significantly ($p > 0.25$) from the expected frequency distribution. The observed frequency distribution differed significantly from the random distribution (chi-square = 11.74; DF = 5; $p < 0.05$), as did the expected distribution (chi square = 158.9; DF = 5; $p < 0.001$).

Mean observed burrow distance to the closest wash was compared to the mean distance from the randomly located burrows (table 6).

Comparisons for the sparse wash and Hiri/Amdu communities were not done because they would be biologically meaningless or had too low a sample size, respectively. For all burrows, and for burrows found in either the Latr/Amdu or mixed communities, no significant differences between random and observed wash distances were detected. Thus, observed tortoise burrows were not located closer to washes than a set of random points predicted. However, examination of the spatial pattern (fig. 1) reveals a lack of burrows deep within Latr/Amdu and Hiri/Amdu areas which were furthest away from any possible wash influence.

Past observations seemed to indicate a correlation between burrow location and the presence of the edge of the *H. rigida* distribution (Baxter and Stewart 1986). The approximate distribution of observed burrows to this edge may be seen in figure 1. Mean edge (ecotone) distance of observed burrows was compared to that of random sites (table 7). Highly significant differences in ecotone distances were found in both communities, and also when combined. Thus, burrows were found closer to the ecotone than a set of random points.

Tortoise Captures

Similar analyses were performed for tortoise capture sites. There were a total of 120 tortoise captures and recaptures of 41 individual tortoises. The observed captures per grid, along with the randomly located capture frequencies (same points used for random burrow sites) were compared against expected values derived from the Poisson distribution (table 8). Observed capture sites showed a statistically significant departure from Poisson expected frequencies by the goodness-of-fit test ($p < 0.05$).

Frequencies of capture sites in each plant community were compared against expected values gener-

ated by community abundance (table 9). Observed distributions for both all captures, and for captures of active tortoises (those found outside of burrows) differed significantly from expected. These two observed distributions did not differ from each other (chi-square = 0.5385; DF = 5; $p > 0.99$), yet differed significantly from the randomly generated distribution (chi-square = 18.957 and 19.556, respectively; DF = 5; $p < 0.005$). Thus, tortoise captures were not found across the plot in a random fashion as would be predicted

by a set of randomly generated points. Habitat preference for washes was seemingly indicated, as was a lack of preference for Hiri/Amdu areas. These results also gave further support to the non-randomness exhibited in the Poisson analyses.

To further examine this apparent non-random distribution of capture locations, the mean observed capture distance to washes was compared to that of the randomly located sites (table 10). When all capture sites, or captures within the mixed community were considered, a significant

Table 8.—Distributions and significance of tortoise captures per grid (Poisson, $n = 64$).

Number of captures/grid	Number of grids		Expected values	
	random	observed	random ^a	observed ^b
0	6	19	4.95	9.97
1	11	17	12.67	18.54
2	15	15	16.21	17.23
3	15	4	13.83	10.68
4 or more	17	9	13.59	5.54

^a $P > 0.90$

^b $P < 0.025$

Table 9.—Summary of frequency of captures compared to plant community abundance.

	Plant community ^a					
	Sparse Wash	Hiri/Amdu	Mixed	Latr/Amdu	Wash	Other
% of plot	5.6	4.0	37.2	50.6	0.2	2.4
Random ^b						
observed ($n=164$)	14	6	55	76	8	5
expected	9.2	6.6	61.0	83.0	0.3	3.9
Observed (all) ^b						
observed ($n=120$)	14	1	33	48	23	1
expected	6.7	4.8	44.6	60.7	0.3	2.9
Observed (active) ^b						
observed ($n=81$)	9	1	20	32	18	1
expected	4.5	3.3	30.1	41.0	0.2	1.9

^aSee text for explanation of community names.

^b $P < 0.001$

difference between random and observed locations was demonstrated. However, mean distance to washes within Latr/Amdu sites was not significantly different from the random set of points, possibly because the Latr/Amdu communities were generally located further away from washes, as well as the high variation in observed Latr/Amdu distances. These results, along with the results of the community analysis above, seemed to indicate a high degree of tortoise activity near the washes.

Distances to the edge of the *H. rigida* were compared between randomly generated and observed capture locations (table 11). Highly significant differences in mean distances were demonstrated for both the Latr/Amdu community, and for captures found in the mixed and Latr/Amdu communities combined. Cap-

tures within the mixed community alone were not significantly different from randomly generated locations. It seems then that captures, like burrows, were generally not found far within Latr/Amdu areas, but tended to be near its edge with the *H. rigida* distribution (i.e. the mixed community). Because there was no difference within the mixed community alone, differences from random for captures within the mixed and Latr/Amdu communities combined were probably significant due to the higher number of observations within the Latr/Amdu community biasing the sample. Thus, it seems that tortoises tended to stay either near the washes, the mixed community, or its ecotone with the Latr/Amdu community, and generally were not going far within the Latr/Amdu community.

Discussion

Since the establishment in 1975 of the Desert Tortoise Council, the amount of literature published on the desert tortoise has been considerable. Oddly enough, only a few papers may be found that attempt to say what exactly makes good tortoise habitat.

A paper by Schwartzmann and Ohmart (1978) quantified the frequency of use by tortoises in a number of "habitat types." Their study took place in the Picacho Mountains of Arizona's Sonoran Desert, where tortoises are known to frequent rocky hillsides and are absent from valley bottoms (Fritts 1985). Habitat preferences are just the opposite in the Mojave Desert, and thus their results may not be applicable. Likewise, Walchuck and Devos (1982) studied tortoise habitat, but this was also in the Sonoran Desert of Arizona.

In a draft report, Weinstein et al. (1986) performed several multivariate analyses on the large Bureau of Land Management tortoise database. Several attempts were made to correlate abundance with habitat characteristics. Not only were many of these characteristics derived from the extrapolation of large scale map data, but the best fit analysis was found by designating "corrected sign" of the transects (the dependent variable; not actual population numbers) into arbitrary categories. Indeed, one of the authors (Berry and Nicholson 1984) has shown that roughly one-third of population estimates (7 out of 20 and 4 out of 6) based on sign transects did not agree with intensive plot censuses. Also, Turner et al. (1982) stated that sign transects "...cannot provide the accuracy and precision needed..." In addition, Fritts (1985) stated that such transects are "...subject to error." Thus the accuracy of sign transects are open to serious debate, and although the discriminant analysis showed some promise as a method

Table 10.—Comparison of distance to washes between observed and random capture locations.

Plant community ^a	Mean distance (m (SEM))		t	Degrees of freedom	P
	random	observed			
All communities	96.83 (6.80)	71.86 (9.39)	2.189	258	< 0.05
Mixed	79.54 (9.75)	44.14 (10.61)	2.081	73	< 0.05
Latr/Amdu	132.05 (10.07)	133.66 (15.12)	0.917	117	> 0.50

^aSee text for explanation of community names.

Table 11.—Comparison of distances to ecotone between observed and random capture locations.

Plant community ^a	Mean distance (m (SEM))		t	Degrees of freedom	P
	random	observed			
Latr/Amdu	32.33 (9.09)	18.59 (3.05)	3.389	114	< 0.001
Mixed	38.63 (2.65)	21.05 (4.65)	1.595	42	> 0.10
Combined	34.05 (3.00)	13.99 (2.53)	3.485	157	< 0.001

^aSee text for explanation of community names.

for accessing regional abundances, the nature of the analysis and the underlying assumptions of both the data acquisition and techniques leave much to be desired.

When viewed from the larger scale of regional or even plot area, these data seem to indicate that burrows were found in a random fashion when predicted by burrows per unit area. However, different results may have been obtained by changing the size and shape of the grids. For example, 32 larger rectangular grids may very well have produced different results than the 64 smaller square grids used in this study. In addition, such an analysis said nothing about distributions in relation to habitat characteristics. Therefore, such a test should be used as a starting point and/or support for other tests, and locally is of limited use by itself for describing ecologically meaningful patterns which may exist.

With closer examination, these data also indicate that burrow locations were assembled in a pattern similar to the non-random distribution of plant communities. Within-community examinations revealed patterns of burrow site utilization, and such patterns were strongly non-random. At Sand Hill then, while a majority of burrows were not found in washes, they were often found within easy walking distance to a wash. Very often, burrows were on slopes high above washes, and possibly within its area of influence. They were not found far within either the Latr/Amdu or Hiri/Amdu communities, but were tied strongly to the edge of these communities with the mixed community.

Washes are sometimes cited as being of great importance to tortoise populations (Burge 1978, Hohman 1977, Lowe 1964). However, results of this study indicated that tortoise burrows were not significantly closer to washes than a set of randomly selected sites. Burge (1978) found 207 (26%) of 783 burrows and pallets were associated with washes. Of

these, 56 (27%) were actually within a wash bed. However, Burge apparently eliminated some burrows from the analysis due to their physical characteristics. The discrepancy may be due to the definition used. In this study, wash burrows were defined as such, only if they were actually within the sandy wash bottoms. In this way, burrows which were on wash banks, were counted as being in the plant community of the bank. Burrows located on wash banks, and even further away, may have been associated with the wash, and a reclassification of these burrows may show washes to have a more important influence in burrow analyses. Examinations of the actual burrow distribution (fig. 1) seemed to indicate that they were mostly absent from areas highly isolated from wash influence.

The significance of capture locations in relation to the washes also seemed to refute the burrow/wash results. Washes clearly supported a disproportionate amount of activity in relation to their abundance on the plot. Preliminary investigations of tortoise communities near Kramer Junction, San Bernardino County, have also shown tortoises are probably localizing their activities in the vicinity of washes (Baxter, unpub. data).

Several things may explain the disproportionate amount of captures in the washes. Greater visibility of tortoises in the washes may be a factor. Utilization of highly diverse plant resources there may also contribute to the localization of activity. Finally, washes may simply serve a natural highways for tortoise movements. For instance, several relocated tortoises at Kramer Junction abruptly turned and followed trails and washes upon their release (Baxter, unpub. data). Regardless, these data seem to support washes as an important habitat characteristic for tortoises at Sand Hill. If this population is representative of other Mojave populations, the importance of

washes in potential relocation sites will be highly significant in assuring the best chance of survival for the relocatees. Further, impacts to washes may have highly significant impacts on a population if it is localizing its activities there.

These data support the importance of large woody shrubs (i.e., *L. tridentata*) for successful burrow construction at this site. Similar results have been reported by Burge (1978) who found 72% of "cover sites" associated with shrubs. Berry and Turner (1984) found 75% of juvenile burrows associated with bushes. Support for the burrow roofs and added protection from predators are likely reasons for this association. Regardless, the absence of *L. tridentata* from the Hiri/Amdu community is probably a major reason for the tortoises not utilizing those areas. Unsuccessful burrow construction by virtue of the sandier soils is another possibility. This latter assumption is supported by the Weinstein et al. (1986) analysis which showed "soil diggability" as a highly significant regression variable.

However, the lack of burrows deep within Latr/Amdu communities is not explained by the spatial abundance of *L. tridentata*. The high frequency of burrows and captures point out that something is being sought there by the tortoises. Yet, deep ventures within these areas apparently do not provide resources that are unavailable at their edges. Perhaps the higher levels of soil calcium found there are being utilized. Tortoises must support a massive, ossified shell, as well as lay eggs, and calcium may be a very important nutrient. Tortoises have been observed eating dirt (geophagy) and then producing "sand scats," and calcium levels have been hypothesized as an explanation for this behavior (Sokol 1971). The lack of calcium in the sand scats tested seems to support this hypothesis.

In contrast, such deep ventures would take the tortoises away from

the distribution of *H. rigida*, and the frequented and diverse washes. Although detailed scat analyses were not performed, field examination of hundreds of scats seemed to suggest that *H. rigida* is a significant dietary component. Turner and Berry (1986) found *H. rigida* as a part of the diet of tortoises near Goffs, California.

It would seem then that tortoises in this area are exhibiting some characteristics similar to "edge" species. That is, tortoise activity is centered on the two communities with the highest vegetational diversity that border extensive areas of *H. rigida*. Since burrows are closely associated with *L. tridentata*, they in turn are found primarily along the only highly diverse ecotone of the *H. rigida* distribution where *L. tridentata* importance is the highest. This importance of *H. rigida* and *L. tridentata* is further shown in appendix 1. The two communities where tortoises were not found (i.e., deep Latr/Amdu and Hiri/Amdu) each lack one of these species. The assumption that they are focusing on high diversity areas is further supported by Weinstein et al. (1968) which shows "food availability" as the single most significant regression variable. Finally, Speake (1986) reports that for the gopher tortoise (*G. polyphemus*), "Edge habitats or ecotonal areas appear important to tortoises. In each habitat type except oldfields tortoises tended to cluster near the edges. In general, the more edge availability in a given habitat, the higher the tortoise density."

In summary, tortoises utilized the environment at Sand Hill in a mostly non-random fashion. Tortoise captures were spread out between two communities of highly diverse resources, with clustering occurring at either edge. Tortoises frequented washes and the ecotonal edge of the Latr/Amdu community, with many found in the intermediate mixed community. Tortoises were not found deep within Latr/Amdu or Hiri/Amdu areas. Burrows were

found close to the ecotone of the mixed and Latr/Amdu communities. Burrows were not found closer to washes than randomly located burrows, although this point is far from clear. Burrows were located close to the one highly diverse edge of tortoise activity area where the importance of *L. tridentata* and soil calcium were the greatest, and were not found in Hiri/Amdu areas where *L. tridentata* was absent, and soils were the most unconsolidated.

Non-randomness in tortoise populations is especially important for the management considerations of relocation. Clearly, despite the best efforts of concerned managers, the use of the deserts will continue to increase and the frequency of tortoise relocations will also undoubtedly increase. If tortoise distributions are random, relocation management essentially becomes a search for safe relocation sites roughly similar to the "parental" area. No special considerations of unique habitat types are required. If on the other hand they are not, then the relocation site(s) must include such high-use habitats as those found in the parental site. In addition, severe disturbance of such favored habitats will in turn have severe impacts on the populations, particularly if small.

This study indicates that the non-randomness exhibited by the Sand Hill tortoises is probably a function of the non-randomness of highly diverse plant assemblages and edaphic characteristics. Thus, the presence of diverse land forms and their associated plant communities and diverse edges within future relocation sites should be of significant importance to the manager. Areas which "look good" to the relocation manager may not supply the needed resources for the relocatees. These data are in need of further support however. If such patterns are exhibited in other populations, biologists and managers may use such techniques to successfully determine possible habitat requirements, and help insure the survival

of one of the Mojave's most enigmatic species.

Acknowledgments

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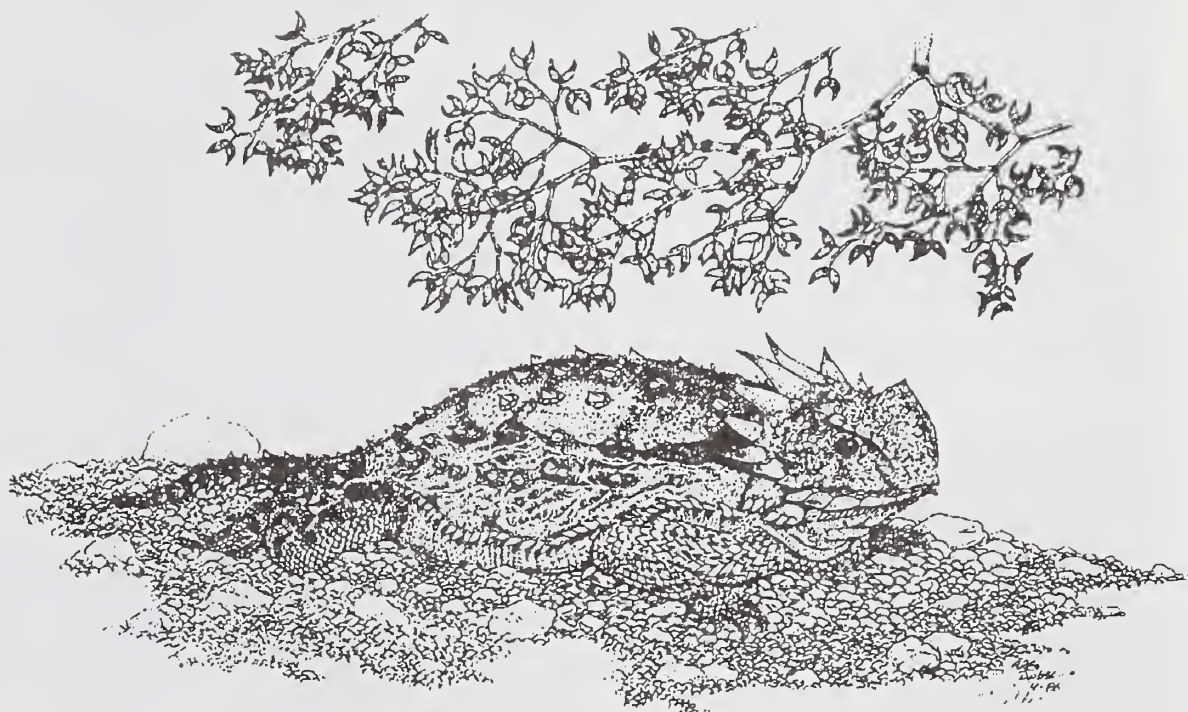
Appendix 1
Summary of Importance Values¹ From Plant Transect Data.

Species	Plant Community ²				
	1	2	3	4	5
Bare Ground	128.2	113.8	110.3	114.7	95.5
<i>Schismus barbatus</i>	64.9	51.8	49.1	26.8	42.6
<i>Larrea tridentata</i>	16.5	—	21.6	36.7	6.7
<i>Ambrosia dumosa</i>	11.8	11.5	27.9	23.8	4.3
<i>Hilaria rigida</i>	2.9	59.9	27.3	—	6.7
<i>Erodium texanum</i>	11.9	6.8	10.2	26.4	19.3
<i>Malacothrix</i> spp.	7.4	29.1	26.1	36.2	10.5
<i>Eriogonum</i> spp.	7.0	—	2.6	13.1	6.6
<i>Hymenoclea salsola</i>	11.1	—	—	2.7	26.4
<i>Amsinckia</i> spp.	15.3	—	—	9.8	2.2
<i>Oenothera deltoides</i>	6.4	—	—	4.8	13.6
<i>Baileya multiradiata</i>	2.0	6.8	6.5	—	—
<i>Abronia villosa</i>	—	5.6	2.2	—	2.1
<i>Bromus rubens</i>	—	—	—	2.7	2.2
<i>Langloisia Matthewsii</i>	4.9	—	—	2.6	—
<i>Langloisia Palmeri</i>	2.3	—	—	—	—
<i>Oryzopsis hymenoides</i>	—	—	2.5	—	—
<i>Eriophyllum Wallacei</i>	2.0	—	—	—	—
<i>Menodora spinescens</i>	2.9	—	—	—	5.7
<i>Lesquerella Palmeri</i>	2.3	—	—	—	3.1
<i>Salazaria mexicana</i>	—	—	—	—	3.0
<i>Dalea Fremontii</i>	—	—	—	—	10.6
<i>Cucurbita foetidissima</i>	—	—	—	—	2.3
<i>Euphorbia polycarpa</i>	—	—	—	—	2.0
<i>Isomeris arborea</i>	—	—	—	—	3.4
<i>Prunus fasciculata</i>	—	—	—	—	6.7
<i>Spheralcea ambigua</i>	—	—	—	—	2.6
<i>Salvia columbariae</i>	—	—	—	—	4.0
<i>Phacelia</i> spp.	—	—	—	—	2.2
<i>Petalonyx Thurberi</i>	—	—	—	—	2.6
Unknown composite #1	—	2.9	2.3	—	7.3
Unknown composite #2	—	—	2.3	—	—

¹Importance value = relative density + rel. domin. + rel. freq.

²Plant community: See text for description of community names; Meadow and bare areas not listed; 1 = Sparse Wash; 2 = Hiri/Amdu; 3 = Mixed; 4 = Latr/Amdu; 5 = Wash.

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Changes in a Desert Tortoise (*Gopherus agassizii*) Population After a Period of High Mortality¹

David J. Germano² and Michele A. Joyner³

Abstract.—An apparent high rate of mortality for desert tortoises at the Piute Valley in southern Nevada between 1979 and 1983 significantly decreased mean carapace length and average age of the population by 1983, but not density. By 1987, average size and age of the population had increased and density remained stable.

Chelonians, as a group, are characterized by high rates of adult survival, delayed maturity, and low rates of juvenile survival (Wilbur and Morin 1988). Many chelonians live a long time after reaching adulthood (Gibbons 1987), potentially leading to a long period of reproduction offsetting low juvenile survival (Wilbur and Morin 1988). The desert tortoise (*Gopherus agassizii*) (fig. 1) is an herbivorous chelonian of the desert Southwest that exhibits these population traits (Berry 1986, Luckenbach 1982, Osorio and Bury 1982, Turner et al. 1984, 1986). In 1983, a large number of desert tortoise skeletons were collected from a study plot located in southern Nevada and deaths were believed to have occurred since the initial census in 1979 (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las Vegas, NV). It was reported that since 1979, mean carapace length of the population decreased, sex ratio had become male biased, and that population density

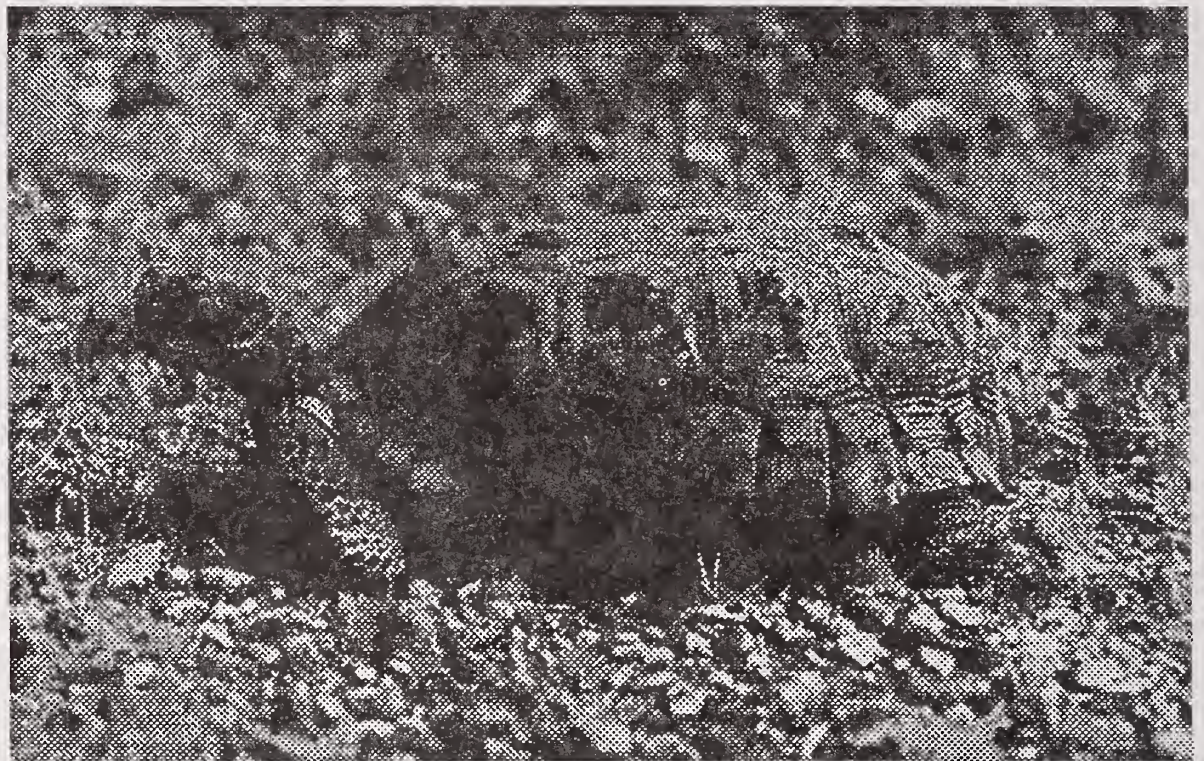


Figure 1.—A large male desert tortoise (*Gopherus agassizii*) from the Piute Valley permanent study plot.

decreased, and that these changes occurred because long-term grazing of this plot by cattle weakened tortoises to such a degree that decreased forage production resulting from below-average rainfall in 1981 killed many individuals (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las Vegas).

We recensused this population in 1987 in order to determine changes that might have taken place since 1983 in age distribution, size distribution, sex ratios, and population density in order to address the following questions: Of what significance are such periods of high mor-

tality to the populations' probability of survival? How do desert tortoise populations respond to high rates of mortality? Are changes in population demographics long-lasting? Can we predict future changes in desert tortoise populations? We also reassess possible causes of the high rate of mortality between 1979 and 1983.

METHODS

Study Area

The 2.59 km² plot is located in the Piute Valley of southern Nevada in

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the eastern Mojave desert (fig. 2). Vegetation is Mojave desert scrub dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) over the southeastern 2/3 of the plot grading into an area with an overstory of Mojave desert yucca (*Yucca schidigera*) in the northwestern third (fig. 3).

Field Methods

The population was censused between April and June 1979 by the Bureau of Land Management (unpublished report, A. Karl, BLM, Las Vegas, NV) and again between April and June 1983 by the Nevada Department of Wildlife (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las Vegas, NV). Each tortoise encountered was measured, weighed, marked, its sex determined, and its location, behavior and general

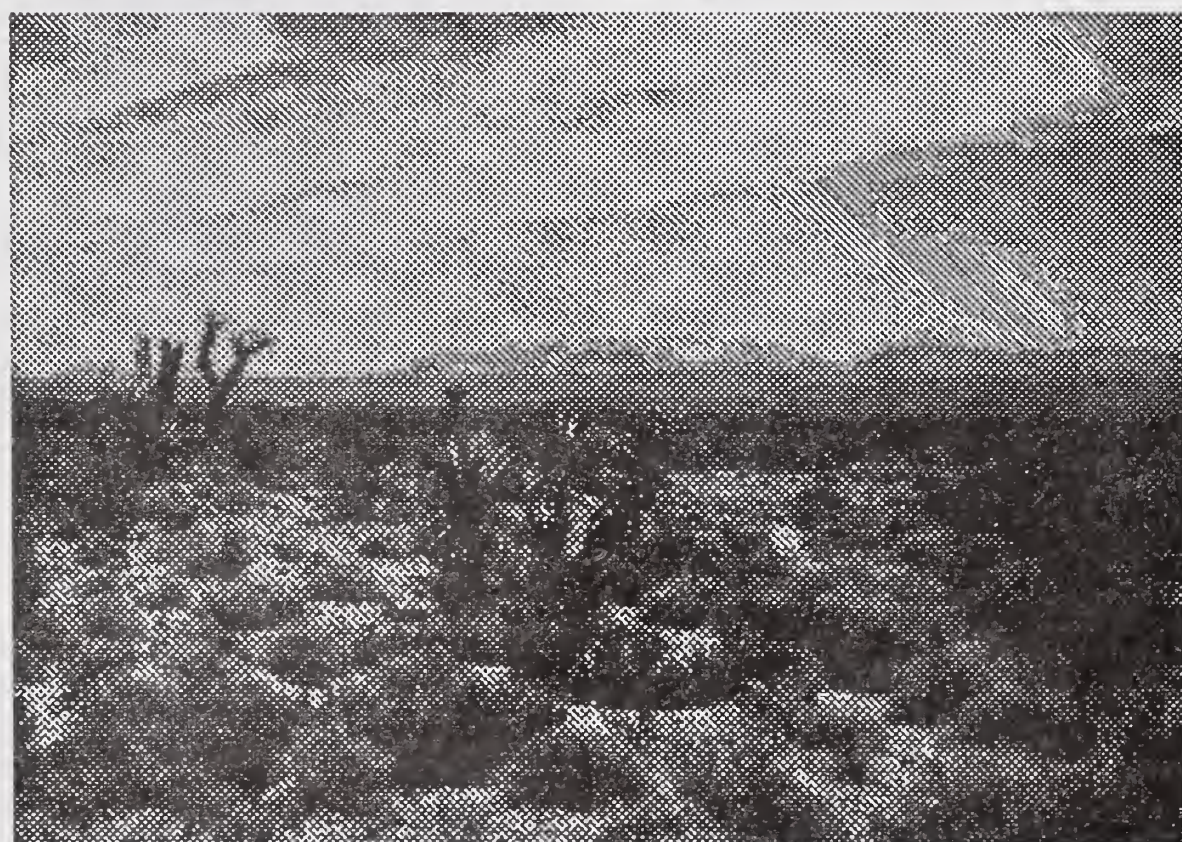
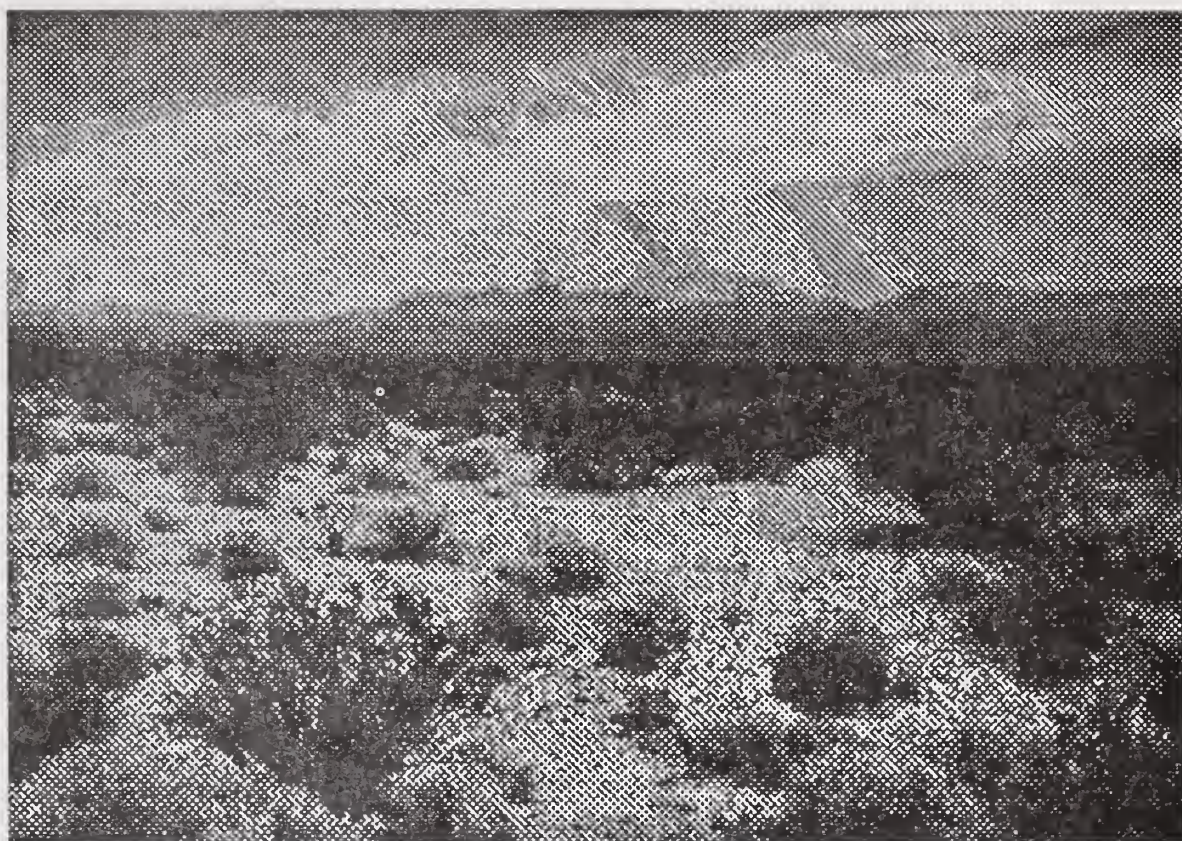


Figure 3.—Creosote bush and white bursage are the most conspicuous plants of much of the study plot (top) with Mojave yucca abundant in the northwestern portion (bottom). Other abundant plants at this site are California buckwheat (*Eriogonum fasciculatum*), rayless goldenhead (*Acamtopappus sphaerocephalus*), *Opuntia* spp., bush muhly (*Muhlenbergia porteri*), gig galleta (*Hilaria rigida*), six-week fescue (*Festuca octoflora*), filaree (*Erodium cicutarium*), desert dandelion (*Malacothrix glabrata*), and *Chaenactis* spp.

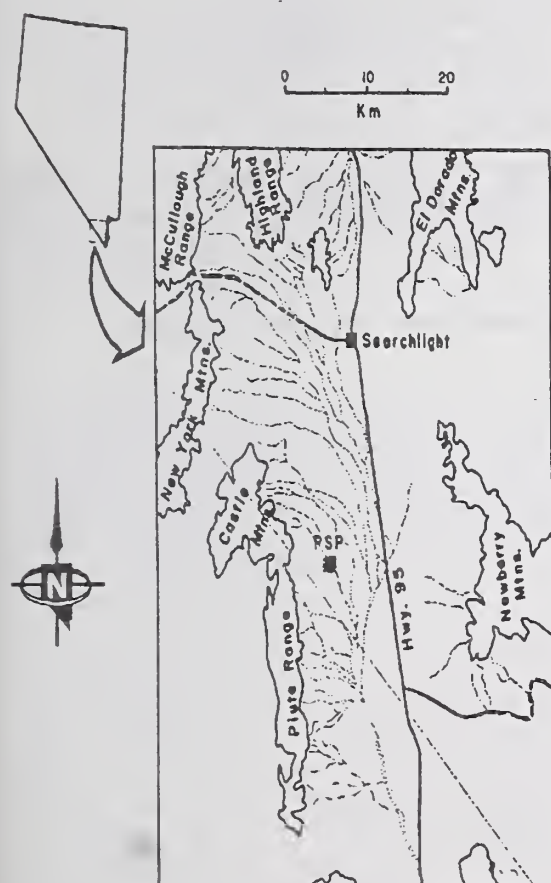


Figure 2.—The location of the desert tortoise permanent study plot (PSP) in the Plute Valley of southern Nevada. The dashed and dotted lines show major washes.

condition noted. Shells were collected and are catalogued in the Museum of Southwestern Biology, University of New Mexico, Albuquerque.

We recensused the plot 13-27 May and 18-25 August 1987. We collected similar data on tortoises, but included making casts of the second costal scute using dental casting ma-

terial (Galbraith and Brooks 1987). Measurements of growth rings from the impressions on the casts were taken.

Growth rings of desert tortoises have been found to be valuable for determining age and growth histories of many individuals (Germano 1988). Shells were collected and deposited in the Museum of Southwestern Biology.

Data Analysis

Density

Densities in 1979 and 1983 were determined by the investigators who conducted the censuses using the Schnabel estimator. This method involves making periodic estimates of density during the census based on the number of marked and unmarked animals found (Tanner 1978). Because of immigration into the plot, we reestimated density for 1983 using the Jolly-Seber estimator (Tanner 1978), which does not assume a closed population.

As a first approximation of density for 1987, we used a simple mark-recapture estimator with May as the period of marking animals and August as the recapture period. Only 1/2 the plot was recensused in August because of time constraints. Density was computed for this half of the plot.

Carapace Length Distributions

Carapace lengths (CL) of individuals were plotted and mean CLs computed for live tortoises and remains for each census year. Mean CLs of the total population, tortoises >180 mm CL, and tortoises ≤180 mm CL were compared among years using anova with comparisons among means using Scheffe's multiple comparisons test.

Age Distributions

Ages of individuals were plotted for live tortoises and remains and mean ages compared in a manner similar to CLs. Ages of skeletons and 1987 live tortoises were determined for most individuals using scute annuli, a technique that is accurate up to 20-25 years (Germano 1988). Several individuals were considered to be older than the number of easily seen annuli based on non-growth since last capture, or scute edge beveling, which indicates continued slow growth. These individuals were categorized as >25 years old.

Ages were estimated for live tortoises found in 1979 and 1983 using an age-CL regression ($\text{Age} = 0.106 \text{ CL} - 3.82$). The number of scute annuli is well correlated with CL ($r^2 = 0.908$, $n = 150$), although the relationship is less accurate in larger individuals. We corrected for the presence of older individuals in our estimates by assigning a portion of adults of various sizes to the >25 age category based on the percentage of adults that were into this category from the 1987 live and 1983 and 1987 shell groups.

Mortality Rates

Age-specific mortality rates were determined for 1979-1983 and 1983-1987 using the equation $q_x = (k [f_x]) / g_x$, where q_x is the mortality rate per year for age x , k is the per capita mortality rate of the population, f_x is the proportion of animals age x that are known to have died in the past year, and g_x is the proportion of animals of age x in the preceding live population (Fryxell 1986). In order to compare mortality rates to age distributions, we determined mortality rates for age groups 0-14 years, 15-27 years, and >25 years. The per capita mortality rate was divided by 4 to obtain the yearly mortality rate for each time period.

Sex Ratios

Sex ratios were compared among live tortoises and shells. Sex was assigned to tortoises ≥180 mm CL based on secondary sex characteristics or, in some instances, for males >170 mm CL when plastron concavity was obvious. Sex can be determined reliably in desert tortoises based on shell characters after 180 mm CL (unpublished report, F. Turner and K. Berry, Southern California Edison Co., CA) and female tortoises in this part of the Mojave desert reproduce at 189 mm CL (Turner et al. 1986), indicating that sexual maturity probably occurs between 180-190 mm CL. Ratios were tested for deviation from a 1:1 sex ratio with Chi-square analysis ($p < 0.05$).

CL/Weight Regressions

Carapace length to weight regressions were constructed for 1979 and 1987 tortoises based on the logarithmic transformation of both variables. Data for 1983 were not available. Slopes were tested against 0 and against each other using t -tests (Sokal and Rohlf 1981).

Growth Rate Comparisons

Individual growth was compared among 1987 live tortoises and shell groups in two ways. Growth rings were compared among groups using mean annual widths (AW) and mean percent growth for rings 1-24 (See Germano 1988 for a description of growth ring measurements). Percent growth for a ring is $\text{AW} / \text{estimated CL for the preceding year}$. CLs were estimated using the length of growth rings from the second costal scute, which are highly correlated to CL ($r^2 = 0.96$, $n = 174$). Growth estimates based on annuli have been found to accurately reflect carapace growth in gopher tortoises (Landers et al. 1982) and desert tortoises (Germano In

Press). Means of these variables for each ring were compared among groups using the nonparametric

Wilcoxon sign test. We also compared the mean AW and mean percent growth of the last two growth rings for the shells found in 1983 to the mean AW and mean percent growth of the 1980 and 1981 growth rings from live tortoises found in 1987 using *t*-tests.

Climate Analysis

Climate was analyzed using weather information from Searchlight, Nevada. Data were compared for 3 time periods; 1970-June 1979, July 1979-1982, and July 1979-July 1987. Means and variances of rainfall, both annual and winter, were compared among time periods. Mean monthly temperatures were compared among time periods and temperatures below freezing were analyzed for duration and relation to unusually warm winter daily highs.

RESULTS

Density

Tortoise density was estimated to be 50/km² in 1979 and 72/km² in 1983 by the authors of these censuses. Eighty-four and 81 tortoises were found in 1979 and 1983, respectively. We reestimated the 1983 density to be 44 tortoises/km². We estimated the density in 1987 to be 59 tortoises/km² (95% confidence intervals, 19-173). We found 48 tortoises in 1987, 33 in May and 19 on the southern half of the plot in August, of which 4 had been marked in May.

Carapace Length Distributions

Distributions of CLs of live tortoise populations varied significantly for each census (fig. 4). Mean CL was significantly smaller in 1983 than in either 1979 ($p < .05$) or 1987 ($p < .05$). Mean CLs in 1979 and 1987 were not significantly different, however ($p > .05$, table 1). No significant differences were found among mean CLs for adults (≥ 180 mm CL). Adults comprised 58% of the 1979 population, 37% of the 1983 population, and 60% of the 1987 population. The mean CL of non-adults (< 180 mm CL) was significantly smaller in 1983 than 1979 ($p < .05$), but was not significantly different than 1987 ($p > .05$,

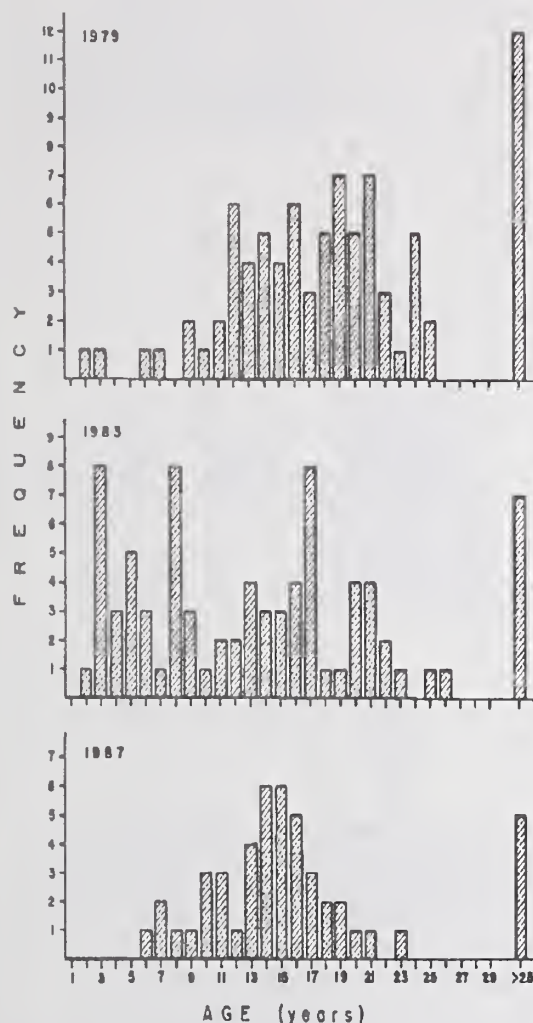


Figure 4.—Population size distributions for live desert tortoises from the Piute Valley permanent study plot. Mean carapace lengths and sample sizes are given in table 1.

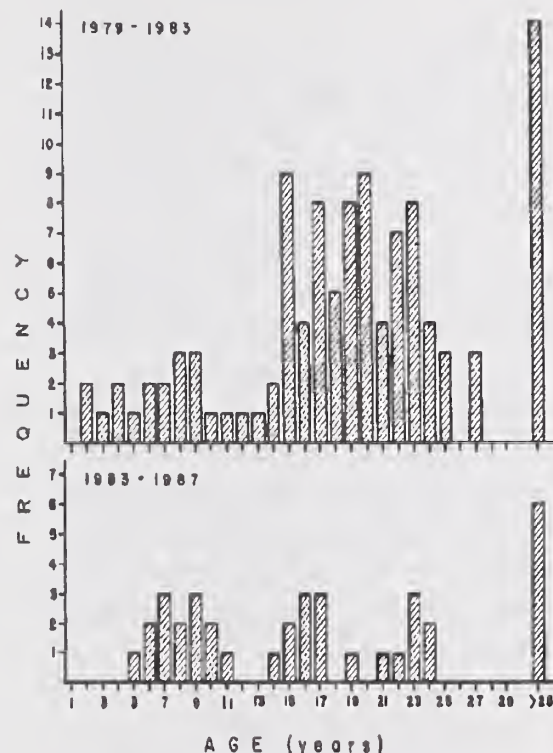


Figure 5.—Population size distributions for desert tortoises found dead in 1983 and 1987 from the Piute Valley permanent study plot. Mean carapace lengths and sample sizes are given in table 1.

Table 1.—Mean carapace lengths (mm) of tortoises from the Piute Valley permanent study plot. Standard deviation and sample size are given below the mean.

Group	All tortoises	>180 mm CL	% of total	<180 mm CL	% of total
1979 live	186.8 (44.0, 84)	217.1 (21.0, 49)	58	144.5 (30.8, 35)	42
1983 live	148.2 (59.6, 81)	211.8 (24.9, 30)	37	110.8 (38.3, 51)	63
1987 live	181.1 (46.6, 48)	213.8 (20.0, 29)	60	125.8 (37.8, 19)	40
1983 shells	197.6 (93.3, 108)	212.9 (22.6, 84)	78	106.4 (39.0, 24)	22
1987 shells	165.4 (58.1, 37)	216.3 (19.4, 18)	49	117.2 (36.9, 19)	51

table 1). The mean CL of non-adults was not significantly different between 1979 and 1987 ($p>.05$).

Remains of 37 tortoises were found in 1987 compared to 109 found in 1983 (fig. 5). Ten shells were found in 1979. CLs of remains were not significantly different ($p>.05$), although mean CL in 1983 was considerably larger than for 1987 (table 1). Mean CLs of adult remains in 1983 and 1987 were similar, as were non-adult CLs, but adults comprised 78% of the 1983 collection and only 49% of the 1987 collection. The mean CL of remains from 1983 was not significantly different from the mean CL of live tortoises in 1979 or 1987, but was significantly larger than live tortoises in 1983 ($p<.05$). Mean CL of remains from 1987 was not significantly different than any live tortoise means.

Age Distributions

Ages of tortoises varied significantly among years (table 2). Changes in age distributions of live tortoises were similar to the changes seen for CLs (fig. 6). The estimated mean age for 1979 was significantly older than 1983 ($p<.05$) but not 1987 ($p>.05$). Mean age for 1987 was not significantly different than 1983 ($p>.05$), but non-adults were significantly older ($p<.05$). Mean age of 1983 remains was significantly older than 1983 live tortoises ($p<.05$), but was not significantly different than 1987 live tortoises or remains ($p>.05$, fig. 7).

Mortality Rates

Death rates for 1983-1987 were lower than for 1979-1983. Per capita mortality rate (k) for 1979-1983 was 0.21/year ($N = 130$) and was 0.08/year for 1983-1987 ($N = 115$). Mortality rates dropped for all age classes after 1983. For 1979-1983 mortality rates were 0.145/year for 0-14 year olds, 0.247/year for 15-25 year olds, and 0.195/year for tortoises >25 years. For 1983-

1987 mortality rates were 0.061/year for 0-14 year olds, 0.093/year for 15-25 year olds, and 0.103 for tortoises >25 years. Mortality rates for all adults (15-25 years and >25 years) for 1979-1983 was 0.240/year and for 1983-1987 was 0.103/year.

Sex Ratios

Sex ratios of live tortoises show an increasing proportion of males (table 3), although only 1987 showed a significantly biased sex ratio. When the 1987 sex ratio was analyzed by size, 92% of tortoises >220 mm CL were males, whereas only 53% of tortoises 180-219 mm CL were males (table 3). When analyzed by age, 63% of tortoises ≥ 20 years were males, but 71% of tortoises of known sex between 13-19 years were males, a significantly higher proportion than females. The sex ratios of dead tortoises were not significantly different than 1:1 (table 3).

CL/Weight Regressions

The regressions of weight against CL had significant slopes for 1979 and

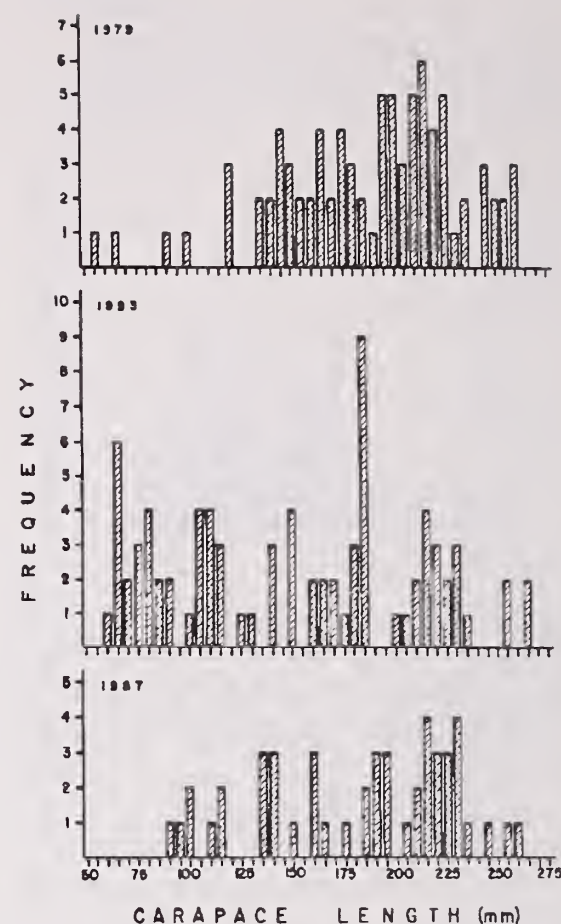


Figure 6.—Population age distributions for live desert tortoises from the Piute Valley permanent study plot. The 1979 and 1983 age distributions are estimates based on a carapace length to annulus number regression. A proportion of adults were placed in the >25 age category based on the proportion of adults in this category from the age distributions for which ages were assigned by annuli counts. The 1987 age distribution is based on annuli counts.

Table 2.—Mean ages of tortoises from the Piute Valley permanent study plot in southern Nevada. Standard deviation and sample size are given below the mean. Ages for 1979 and 1983 are estimates based on carapace length (see Methods).

Group	Ages (years)			
	0-27	0-14	15-27	¹ >25
1979 live	16.6 (5.1, 72)	10.9 (3.4, 24)	19.5 (2.9, 48)	— (12)
1983 live	12.1 (6.6, 74)	7.5 (3.7, 41)	18.8 (3.0, 30)	— (7)
1987 live	14.1 (3.8, 43)	11.3 (3.2, 22)	17.0 (2.2, 21)	— (5)
1983 shells	17.0 (6.2, 94)	7.8 (3.6, 22)	19.9 (3.3, 72)	— (14)
1987 shells	14.0 (6.2, 31)	8.4 (2.6, 15)	19.3 (3.5, 16)	— (6)

¹Mean age cannot be determined.

1987 (fig. 8). The regression equation for 1979 is gram weight = $0.000317 \text{ CL}^{2.924}$ ($r^2 = 0.952$, $n = 73$) and for 1987 is gram weight = $0.000505 \text{ CL}^{2.826}$ ($r^2 = 0.969$, $n = 53$). Regression slopes were not significantly different from each other ($p > .10$).

Growth Rate Comparisons

No significant differences were found in a ring by ring comparison of growth between 1987 live tortoises and 1983 remains for either annual widths (AW) or percent growth.

When 1980 and 1981 rings were compared, no significant difference existed between the mean AW for the last two rings of 1983 mortalities ($X = 1.98\text{mm}$, $n = 72$) and the 1980 and 1981 rings for 1987 live tortoises ($X = 1.92\text{mm}$, $n = 79$; $p > .10$).

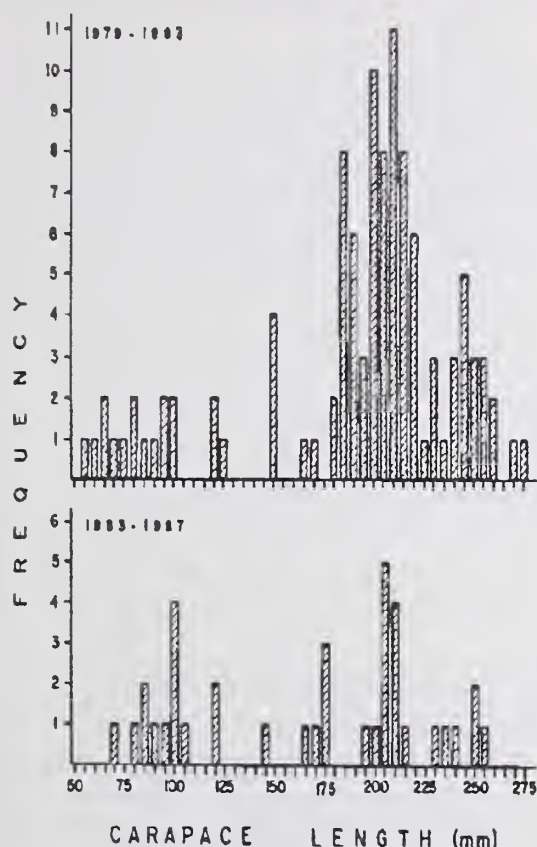


Figure 7.—Population age distributions for desert tortoises found dead in 1983 and 1987 from the Piute Valley permanent study plot. Both the 1983 and the 1987 age distributions are based on counts of annuli.

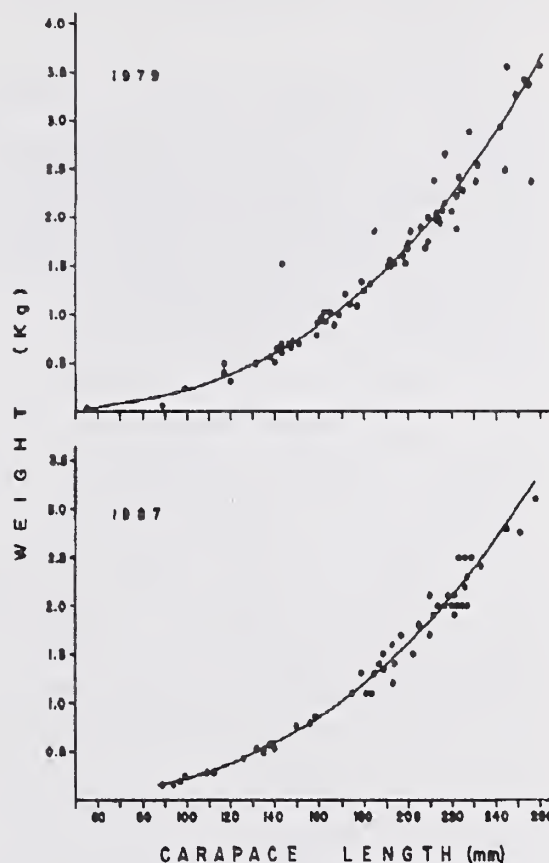


Figure 8.—Regressions of carapace length to weight for desert tortoises found in 1979 and 1987. Slopes of both regressions are significantly different from 0 but not from each other.

Table 3.—Numbers of males to females for desert tortoises from the Piute Valley permanent study plot. Significant departures from a 1:1 sex ratio were determined by Chi-square analysis. The 1987 live totals were sub-categorized by size and age.

Year		Males	Females	Ratio	χ^2
1979	live	24	30	0.88:1	0.667
	shells	4	3	1.33:1	0.001
1983	live	22	11	2:1	3.667
	shells	35	41	0.85:1	0.474
1987	live (total)	20	9	2.22:1	¹ 4.172
	size: 180-219 mm CL	9	8	1.13:1	0.059
	>220mm CL	11	1	11:1	¹ 8.330
	age: 13-19 years	15	6	2.5:1	¹ 3.857
	>20 years	5	3	1.67:1	0.500
	shells	11	6	1.83:1	1.471

¹Significant departure from 1:1 ratio ($p < .05$).

Climate Analysis

Average precipitation were higher between July 1979 and July 1987 than the previous 10 years (table 4). The highest average precipitation was recorded between July 1979 and December 1982. Winter rainfall (October-March) followed the same pattern, with both 1979-1987 and 1979-1982 averages higher than 1970-1979 (table 4). The period 1970-1979 was a drought period with average rainfall 7% below the long-term average of 183.8 mm and 7 of the 10 years were well below average (table 4). When 1978 and 1979 are excluded, average precipitation drops to 129.3 mm, 30% below the long-term average. July 1979-December 1982 averaged 40% higher rainfall than the long-term average with only 1981 experiencing below-average rainfall. Mean monthly high and low temperatures were similar among time periods. No extended periods of freezing temperatures were found for daily readings between 1979 and 1983.

DISCUSSION

Population Parameters

The desert tortoise population in the Piute Valley study plot experienced a high rate of mortality, particularly of adults, between July 1979 and 1983. Related to this event was a significant decrease in the size and age distributions of the population in 1983, although both were returning to 1979 dimensions by 1987. The lower mean age in 1983 is probably a result of increased survival of hatchlings and increased immigration. The increased

survival of hatchlings, as shown by the significant increase of tortoises in the 1-4 age group in 1983, may be due to more favorable conditions because of lower densities just after the high rate of mortality, or to optimal climatic and habitat conditions.

It is possible that the greater numbers of smaller tortoises found in 1983 could have resulted from better search effort for these sizes (Berry and Turner 1984), but we censused the plot carefully in 1987, specifically looking for small tortoises, yet we found relatively few. While we do not doubt that young are missed because of their inconspicuousness, we believe that the changes in size and age distributions between 1979 and 1987 reflect actual population changes.

The size and estimated age distributions for 1983 indicate that a significant number of smaller and younger tortoises came into the plot between 1979 and 1983. Judging by the male-dominated sex ratio after 1979, immigration largely has been by young males. The biased sex ratios are not due to higher adult male survival since equal proportions of males and females died. Most of the males in the present population are fairly young, although they are large. Male turtles are known to disperse greater distances than females (Gibbons 1986).

Although many turtle populations have biased sex ratios, evolutionary theory indicates that these ratios should be under selective pressure to be relatively even, in most instances (Fisher 1930, Trivers 1972). However, desert tortoise age to maturity is ca. 15 years (Germano In Press, Woodbury and Hardy 1948), therefore a reproductive solution mediated by selection would require hundreds of years.

Censuses in other parts of this valley in 1983 indicate that this high rate of mortality was confined to this plot and areas close by (unpublished report, C. Mortimore and P. Schneider, Nevada Department of Wildlife, Las

Vegas, NV). Differences in sex ratios at this plot may be more a reflection of higher male movement rates compared to females and not to a real difference in numbers of males and females in the population as a whole. Over time the sex ratios may change by movement of females into the plot from outside.

Density may have decreased slightly since 1979, but it does not appear to have changed significantly over the 8 year period, although we recognize the imprecision of these density estimates. The number of tortoises found has decreased in each census, but investigators and time periods in the field have varied, ren-

Table 4.—Annual and winter precipitation (mm) for 1970-1987 and for 3 time periods from the Searchlight, Nevada NOAA Station. Winter precipitation is defined by the months October-March. Means and standard deviations are given for the 3 time periods. Precipitation for 1987 only includes the months of January-July.

Year	Annual total	Winter total	Time period		
			Jan. 1970- June 1979	July 1979- Dec. 1982	July 1979 July 1987
1970	127.76		Annual precipitation		
1971	68.83	30.73			
1972	136.65	17.02			
1973	114.81	179.02			
1974	184.40	54.36			
1975	132.08	100.08			
1976	161.80	82.79	Winter precipitation		
1977	107.70	52.58			
1978	473.71	183.90			
1979	256.54	249.43			
1980	313.44	260.10			
1981	162.81	67.06			
1982	366.10	101.09			
1983	376.68	216.15			
1984	300.48	61.47			
1985	149.35	191.52			
1986	166.88	91.69			
1987	73.66	126.24			

dering this comparison unreliable. We believe that the lower number of live tortoises found in 1987 is due to inexperienced field personnel and the shorter duration of time in the field. The most valid of these density estimates is the Jolly-Seber estimate of 44 tortoises/km², because more assumptions are met with this technique. Unfortunately, estimates cannot be made for the first or last census with this technique. Density estimates, though, are similar in magnitude and we believe this indicates that density has remained relatively stable since 1979. The population must have experienced a decline after 1979 but we believe that increased survival of young and immigration from adjacent non-affected areas has quickly returned the density to 1979 levels.

Mortality Factors

Causes of the high rate of mortality have not been demonstrated. The hypothesis that long-term grazing confounded by a drought in 1981 was the cause of the high number of tortoise deaths is not supported by growth analysis of annuli, CL/weight data, or climate data. Growth did not differ significantly between those that died before 1983 and those that survived to 1987. In addition, the weight to size regressions for 1979 and 1987 were the same and both were almost identical to the regression for tortoises from an ungrazed plot in Nevada (Medica et al. 1975). As for a drought in 1981, average rainfall was only 9% below the long-term average (up to 1987) and was actually at the average, up to 1981, given the drought in the 1970s. Preceding 1981 were 3 years of exceptionally high rainfall. In contrast, rainfall in 1977 was 41% below average and followed many drought years (table 4).

Desert tortoises are known to store water (Nagy and Medica 1986) and may be able to store fat. It seems

doubtful that one average year of rainfall after 3 very good years could cause starvation or lethal dehydration. The 2 years preceding our census in 1987 were below average in precipitation, yet mortality rates dropped. The period 1970-1977 was a drought, yet only 10 shells were found in 1979. If these low rainfall years didn't produce a high rate of mortality that could be detected in 1979, it is hard to imagine that one average year after 3 good years would result in excess mortality. Estimates of yearly adult death rates from 1972-1982 for a population only 42 km south of this site was 1.2%, in an area that has been grazed by livestock for 100 years (Berry and Nicholson 1984a).

Other possible causes for this mortality could have been disease, predation, or flooding. Diseases are known to affect other turtle species in the wild (Jacobson 1980a,b), but no evidence exists for disease as a factor. Many of the shells show signs of chewing by carnivores, although whether this indicates predation or scavenging cannot be determined. Flooding occurred in or near the plot in 1980 and 1982 (unpublished report, J. Jamrog and R. Stager, BLM, Las Vegas, NV). The plot is dissected by numerous washes that are most prevalent in this part of the valley (fig. 2).

The exact cause of the high rate of mortality may never be known. Starvation, disease, flooding, and predation may have all had an effect. No singular explanation is supported by the data. Whatever the causative agent, the population appears to be returning to a density and population structure as occurred before the period of high mortality.

Management Implications

As a long-lived reptile, the desert tortoise is more vulnerable to fluctuations in adult mortality than to similar fluctuations in younger age

groups. Many desert tortoise populations consist of adult segments that usually have yearly survivorship rates of 95-98% (Berry and Nicholson 1984b). High adult survivorship is often coupled with low juvenile survivorship (Wilbur and Morin 1988) and part of the concern for tortoise populations is that they may not have the ability to withstand disturbance because of low juvenile survivorship. Female desert tortoises in the eastern Mojave desert have the ability to lay 2-3 clutches in a season (Turner et al. 1986). The significant increase in 1983 of tortoises 1-4 yr of age suggests more hatchlings have survived between 1979-1983 than previously. As with any other population parameter, juvenile survivorship can vary, and this may lead to periodic additions of greater numbers of young surviving to adult age.

It appears that desert tortoises have the ability to recover from disturbance in some instances. This appears to be what is happening at the Piute plot. Increased juvenile survivorship and immigration are holding the population density stable and the age and size distributions are returning to 1979 dimensions. This kind of recovery may not occur if a disturbance is prolonged or is widespread. Those managing desert tortoises must be aware of the dynamics of each population, but it is apparent that tortoise populations can recover from short-term high mortality.

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A Survey Method for Measuring Gopher Tortoise Density and Habitat Distribution¹

Daniel M. Spillers and Dan W. Speake²

The only tortoise to occur in the southeast, the gopher tortoise (*Gopherus polyphemus*) (fig. 1), is limited to six states. Of these six states, legal protection is offered by South Carolina, Mississippi, Georgia, Florida and Alabama; Louisiana does not restrict the harvest on gopher tortoises at present. The gopher tortoise is now federally listed as threatened in the portion of its range west of the Tombigbee river in Alabama.

During the past several years, an apparent decline of gopher tortoise populations has been noted. Bozeman (1971) and Wharton (1978) noted the rapid loss and alteration of sand ridge habitat, the habitat in which most gopher tortoise populations occur, and argued for the preservation of these habitats not only for gopher tortoises but also for other aspects of their ecological signifi-

cance. Auffenberg and Franz (1982) documented a decline of gopher tortoise populations on specific sites in the Southeast. Landers et al. (1980) found that gopher tortoises have such a low reproductive rate that human exploitation of tortoises can drastically reduce local populations. Landers and Speake (1980) showed that population densities of gopher tortoises can fluctuate widely in response to habitat manipulation or neglect. Other conceivable reasons for this apparent decline were noted by Diemer (1986).

Sand ridge habitat is not only important for gopher tortoises, but also for many other animals that use gopher tortoise burrows for nesting, feeding, or escape cover. Three subspecies of the crawfish-gopher frog complex that are closely associated with gopher tortoise burrows are the dusky gopher frog (*Rana areolata sevosa*), the Florida gopher frog, (*R. a. aesopus*), and the Carolina gopher frog (*R. a. capito*). The threatened eastern indigo snake (*Drymarchon corais couperi*) is dependent on tortoise burrows for winter cover in the northern part of its range (Speake et al., 1978; Landers and Speake, 1980; Diemer and Speake, 1981). Several species of mammals and birds use gopher tortoise burrows, most often as escape cover. Several authors have noted the diversity of animal life (both vertebrate and invertebrate)

Abstract.—An underground closed-circuit television camera and Landsat satellite imagery were utilized in a 2-year study to examine status of the gopher tortoise in southern Alabama. Use of this camera resulted in a complete count of gopher tortoises in the sample transects. The transects were located precisely on standard topographic maps and on Landsat images. An estimation was then made of the amount of each habitat type in southern Alabama based on light reflectance of the vegetation and soil type of the sample transects. Density measurements were then expanded to estimate tortoise numbers for the entire area. This method is effective for estimating gopher tortoise numbers and for determining quantity and location of gopher tortoise habitat.



Figure 1.—A gopher tortoise from southern Alabama.

inhabiting tortoise burrows and the dependence of some species on tortoise burrows for survival (Allen and Neill, 1951; Hubbard, 1894; Hutt, 1967; Landers and Speake, 1980; Speake et al., 1978; Woodruff, 1982).

In view of the apparent decline of gopher tortoise populations, it is important to be able to accurately measure tortoise density in an area and to determine quantity and distribution of suitable tortoise habitat. Tortoise density has been previously estimated by means of a correction factor applied to counts of burrows (Auffenberg and Franz, 1982), digging of burrows, and use of listening devices. Previous methods do not ensure accurate determination of tortoise density without burrow destruction and prohibitive labor. Determination of quantity and location of tortoise habitat is becoming neces-

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sary due to rapid changes in land use and increasing relocation and restocking efforts (Diemer, 1984; Landers, 1981).

The objectives of this study were to develop and employ a method to: (1) accurately measure gopher tortoise density and (2) locate and quantify tortoise habitat in a 24-county area of southern Alabama.

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Methods

Study Area Determination and Questionnaires

Our study area was determined by the reported historical range of the gopher tortoise in Alabama (Mount, 1978; Auffenberg and Franz, 1982). This included 24 counties in the coastal plain of Alabama (excluding the counties west of the Tombigbee river which were surveyed by other researchers). Questionnaires were sent out to wildlife biologists, conservation officers, herpetologists, county agents, soil conservation

agents and other people who were likely to have knowledge of gopher tortoise populations in our 24-county study area. These questionnaires asked for locations of areas that supported or had supported tortoise populations, and names of landowners or other persons who might have additional knowledge of tortoise populations. A map was included with each questionnaire so that locations could be marked. A total of 132 questionnaires was mailed out and 58% were returned.

Soil conservation offices were visited in each surveyed county and further inquiries were made concerning tortoise population occurrence and habitat availability. Areas in each county that had soils with sand to a depth of at least 1 m and that preferably contained a variety of habitat types were delineated on maps. These areas were considered potential tortoise habitat (Garner and Landers, 1981; Landers, 1981; Landers and Garner, 1981) and were used to sample tortoise densities.

After evaluation of the information from the questionnaires, personal interviews, and discussion with soil conservation agents, the 24-county study area was divided into three classes (fig. 2). Class I counties ($n=14$) contained widely distributed gopher tortoise populations and habitat. Class II counties ($n=4$) contained relict or disjunct populations and scattered, spotty habitat. Class III counties ($n=6$) were those in which no tortoise populations could be found.

Sampling Scheme

In Class I counties, regions delineated by the soil conservation agents (sandy soil > 1 m) were located on 1:24,000 scale topographic maps. Within these areas, a reference point for initiation of sampling was chosen from the map which had a variety of habitat types (at least 2) within a 1 km radius of the reference point.

These points were chosen before visiting the site. Where necessary, permission was obtained for sampling on private property.

Upon arrival at the location as many of the following habitat types were located as possible: unburned pine/scrub oak, burned pine/scrub oak, planted pines, clearcuts, old-fields, agricultural fields, pasture, and corresponding edges for each type. The example of each habitat type nearest to the reference point was then sampled.

Belt transects measuring 265×15 m (0.4 ha) were systematically located within the habitat types available; edge transects were centered on and followed the edge. If there were open burrows in the transect, the burrows were examined using the MUTVIC (Miniature Underground Television Inspection Camera) (Speake and Altieri, 1983). This device enabled us to insert a closed-

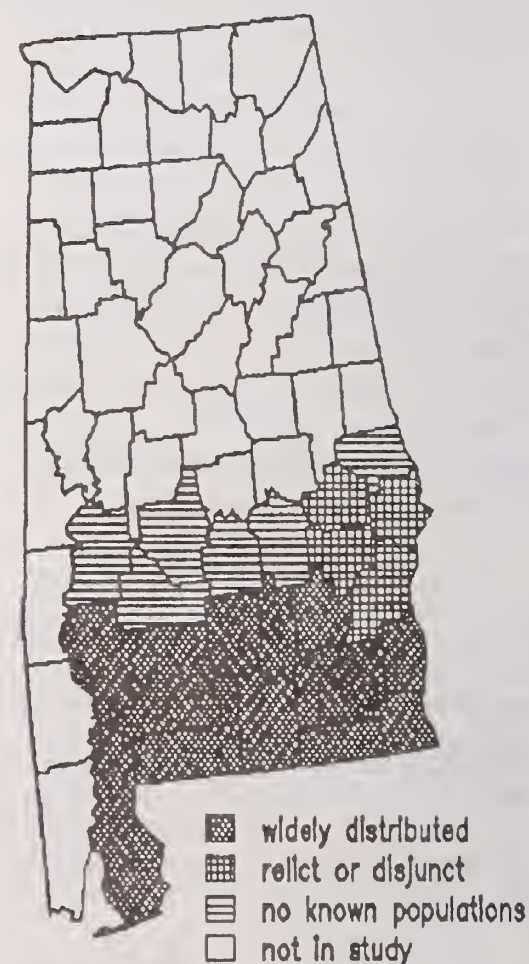


Figure 2.—Distribution of the gopher tortoise in 24 counties of Alabama.

circuit television camera to the bottoms of the burrows and determine if they were occupied (figs. 3-5). Burrow width measurements were made with calipers inserted approximately 70 cm into the burrow. Data gathered for each transect included habitat

type, number of open burrows, number of active burrows (burrows with sign of recent tortoise use), number of tortoises, and width of burrows.

In Class II counties we searched each area where tortoise populations had been reported or where gopher

tortoise habitat (sandy soil > 1 m) existed. Observations were made of the total number of burrows, and total number of active burrows. Since these counties lay along the northern border of the gopher tortoise's range in Alabama, tortoise populations were scattered and did not occur as uniformly in specific habitat types as those populations in Class I counties. Therefore we did not sample here but instead used a correction factor similar to the one described by Auffenberg and Franz (1982). The correction factor (0.67 tortoises/active burrow) was obtained from our sampling of Class I counties by dividing the total number of tortoises by the total number of active burrows. The estimated total number of tortoises for Class II counties was very low (56), and did not significantly affect our population estimate.

Landsat Satellite Imagery

Having measured tortoise density on sample areas of the habitat types, Landsat digital satellite imagery was used to obtain an estimate of the area of each habitat type in Class I counties. Characteristics and usage of this remote sensing technique are described by Anderson, Wentz and Treadwell (1980), Brabander and Barclay (1977), Diemer and Speake (1983), Graham et al. (1981), Taranik (1978a), and Taranik (1978b). The system we used makes a scan of the earth every eighteen days from a geosynchronous orbit. The multispectral scanner operates in seven different wavelengths of light—four visible and three infrared. We used near infrared because it showed vegetation characteristics more clearly. By making several passes, the scanner senses light reflectance based on 0.1 ha pixels. Each 0.1 ha of the earth's surface is assigned 1 of 256 gray values based on its reflectance. Using these gray values we separated the following habitat types based on their spectral signature: unburned

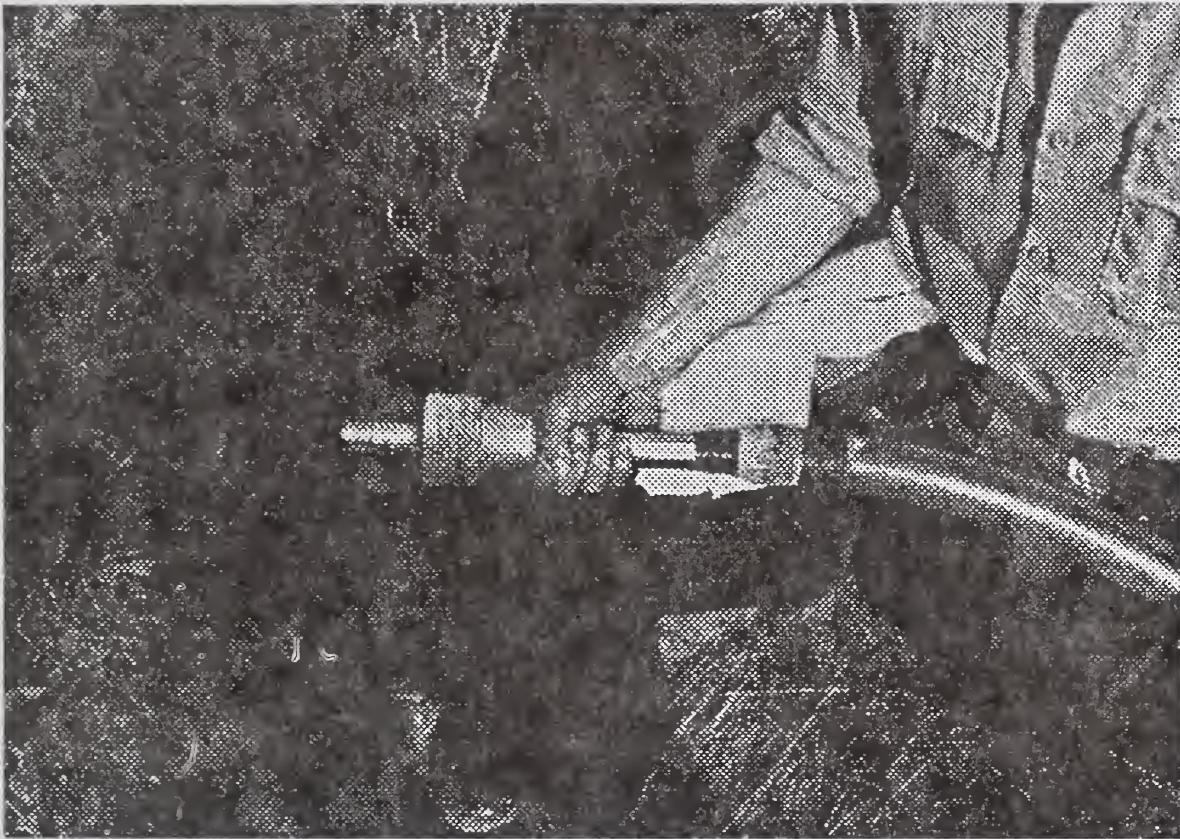


Figure 3.—Closed-circuit television camera with protective glass globe.



Figure 4.—Crew inserting closed-circuit television camera into gopher tortoise burrow.

pine/scrub oak, burned pine/scrub oak, planted pine, old-field, agricultural fields, pasture and composite edge.

Before sampling, we used ground-truthing to determine if it was feasible to attempt to classify each habitat type using Landsat imagery. On 70-0.4 ha sample plots in Baldwin County (10 plots in each habitat type), each plot was correctly classified. Clearcuts were not included because they were a rapidly changing transient stage (1-2 years) leading to planted pine habitat, and as such could not be identified on Landsat images accurately due to their rapid vegetational change. Habitat was considered planted pine if pine was a prominent understory or midstory component (at least 0.3 m tall). Individual edge types were combined because edge transects had similar vegetation characteristics and thus a similar spectral signature. Combined edge habitat was identifiable.

NASA software used with Landsat imagery includes a program for referencing Landsat digital data to any scale map. We referenced our data to standard 1:24,000 topographic maps using known control points. This enabled us to use Universal Trans Mercator coordinates to locate each transect on the Landsat image and obtain the correct gray value for each transect. We then assigned a range of gray values to each habitat type based on the reflectance of the sample transects. The accuracy of the habitat classifications was checked throughout this process.

A polygon was then constructed enclosing all the Class I counties, and areas of each gray value within this polygon were measured. From these measurements we determined the total area for each habitat type in Class I counties.

Data Analysis

We had two concerns relative to data analysis: (1) to derive a population

estimate based on mean tortoise density per hectare multiplied by the estimated area of the respective habitat type, and (2) to identify and locate gopher tortoise habitat.

In order to obtain a population estimate we multiplied the mean density of gopher tortoises per hectare in a specific habitat type by the total area of that habitat type in Class I counties. An allowance was made for standard error of the mean. The habitat totals were then summed to give a final population estimate of the Class I counties.

In addition to these concerns we examined age class structure. Landers et al. (1982) noted that gopher tortoises pass through two general life-history stages before they reach sexual maturity. The juvenile stage lasts until the carapace is approximately 100-120 mm. During the juvenile stage, the shells are very soft and carapacial scutes usually have distinct yellow centers. This stage usu-

ally lasts until about 5 years of age. Juvenile coloration fades and the shells begin to harden during the subadult stage which generally lasts from 5 to 21 years of age. Carapace lengths range from about 120-220 mm. At sexual maturity, body volume has drastically increased and sexual dimorphism is apparent. This occurs at approximately 21 years of age and a carapace length of 230 mm. Alford (1980) established a mathematical relationship between the widths of gopher tortoise burrows and the carapace lengths of their occupants in northern Florida (this relationship has not been thoroughly tested in other states). Using Alford's equation $\log_{10}y = 0.879 \log_{10}x + 0.149$, where y is carapace length and x is burrow width, we used our burrow width measurements of occupied burrows to divide tortoise populations into juvenile, subadult, and adult age classes. We considered age class structure to be an important cri-

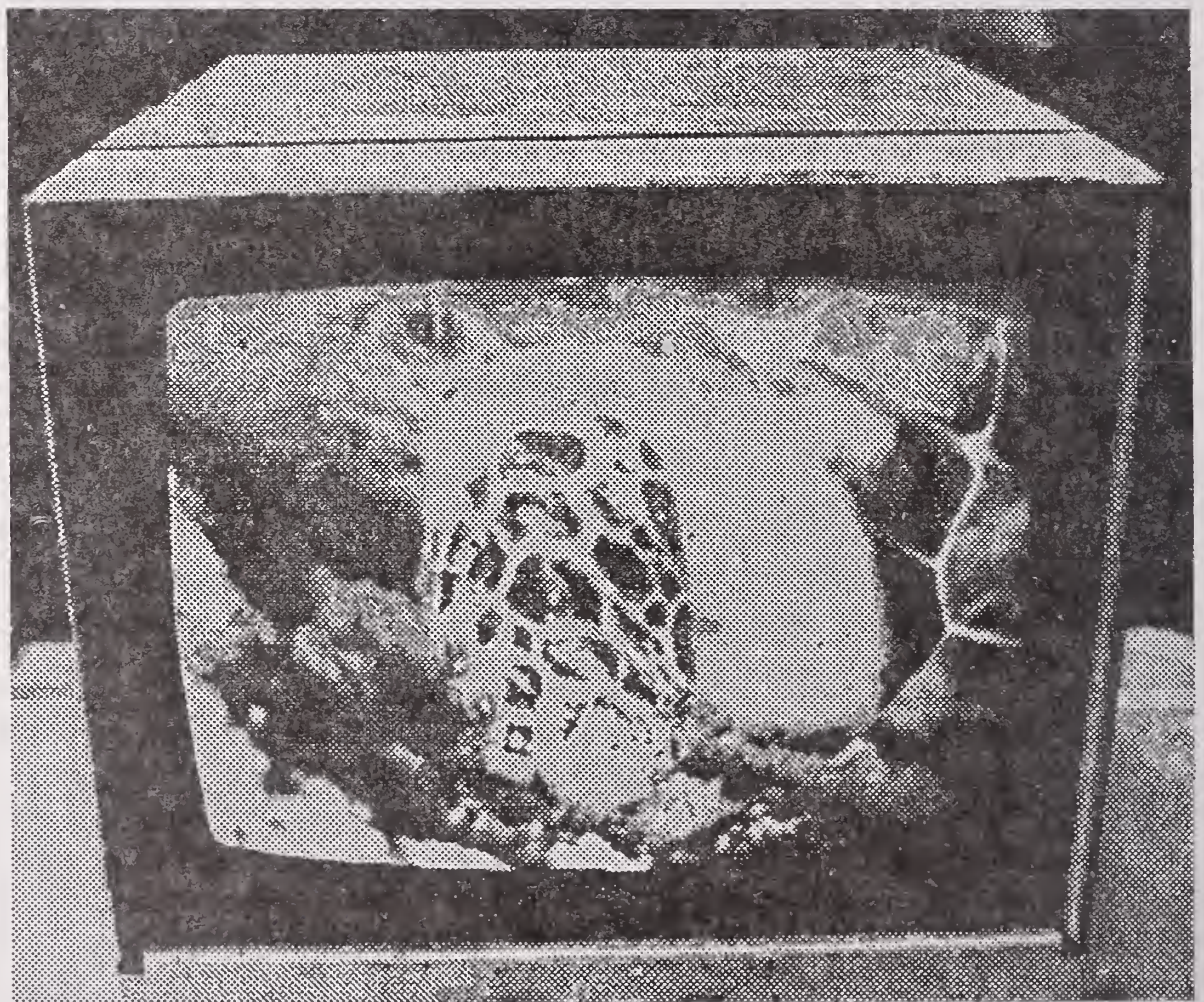


Figure 5.—Closed-circuit television monitor displaying picture of a gopher tortoise inside a burrow.

Table 1.—Summary of sample variables and derived estimates for Class I counties from 339-0.4 ha transects in southern Alabama, 1984-1985.

Habitat	n	Habitat totals			Mean densities/ha			Standard error ^a	Area (ha)	Population estimate
		Open burrows	Active burrows	Tortoises	Open burrows	Active burrows	Tortoises			
Old-field	21	23	17	13	2.72	2.00	1.53	0.47	35,822	207,808 ± 63,836
Planted Pine	17	7	6	5	1.01	0.87	0.72	0.35	99,855	71,896 ± 34,949
Burned Pine/										
Scrub Oak	34	36	13	9	2.62	0.94	0.64	0.27	209,108	133,829 ± 56,459
Edge	129	85	54	34	1.63	1.04	0.64	0.15	102,408	65,541 ± 15,361
Pasture	46	1	1	1	0.05	0.05	0.05	0.05	61,225	3,061 ± 3,061
Agriculture	31	0	0	0	0.00	0.00	0.00	0.00	210,386	0
Unburned Pine/										
Scrub Oak	10	0	0	0	0.00	0.00	0.00	0.00	133,004	0
Clearcuts	51	1	1	0	0.05	0.05	0.00	0.00	—	—
Totals	339	153	92	62					951,808	482,135 ± 173,666

^aStandard error of the tortoise mean density/ha.

teria along with density in evaluating tortoise population viability. Research has not yet revealed an optimum age class structure. Intuitively, in a long-lived animal such as the gopher tortoise, the age class structure of a healthy population would be skewed toward the adult class. The presence of juvenile and sexually mature adult tortoises does definitely indicate recent reproduction.

Results

Gopher Tortoise Densities and Habitat Areas

Tortoise densities and habitat areas were measured in Class I counties. These results are summarized in table 1, which includes sampling variables by habitat type along with estimates derived from sampling.

Age Class Structure

Five percent of the sampled population (n=100 tortoises) were juvenile tortoises, 48% were subadult, and 47% were adults. This structure

shows that there has been recent reproduction, and that there is a large segment of breeding size adults present. This suggests that the potential for successful population maintenance over the estimated 951,808 ha area of tortoise habitat in Class I counties is good.

Discussion

Using the referenced Landsat data and knowing the range of gray values for each habitat type, we were able to examine any area in Class I counties and determine the size and quantity of gopher tortoise habitat units. Using a plotter, figures can be made of all the 0.1 ha pixels that correspond to a given habitat type and then the figure can be overlaid on a map. For our purposes we only needed the area of each habitat type in Class I counties.

This technique has two distinct sources of error. First is the variation of the gopher tortoise densities within habitat types. These variations are inherent in sampling biological populations. In this study the variance was fairly low. Increased sample size would likely lower this

error. The second source of error is in estimating total areas of the habitat types over a large region. Although in our preliminary ground-truthing, Landsat imagery correctly classified all our habitat types (excluding clearcuts and individual edge types), we suspect that when this technique is applied to a large diverse region some areas will be misclassified. Ground-truthing should be done after the classification to determine what percentage has been misclassified, which would allow the researcher to make allowances for this error in final computations.

Conclusions

We found this technique to be useful for measuring tortoise density and for determining quantity and location of tortoise habitat. The error in this technique seems to be less than that for techniques used for censusing most other animals. Although it is difficult to estimate numbers of animals over a large area, it is helpful to be able to accurately measure density in small areas and then extrapolate this density on the basis of a

quantitative measurement of a designated area. This method should be especially valuable for surveys of animals that are habitat specific.

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Evaluation and Review of Field Techniques Used to Study and Manage Gopher Tortoises¹

Russell L. Burke² and James Cox³

Introduction

Of the approximately 107 genera and 267 species of North American reptiles, two species of tortoises have received a relatively large amount of scientific attention. Organizations dedicated to the conservation and protection of the gopher tortoise (*Gopherus polyphemus*) (The Gopher Tortoise Council) and the desert tortoise (*G. agassizi*) (The Desert Tortoise Council) attest to heightened levels of amateur and scientific interest in these species. Past bibliographies (Diemer 1981, Douglass 1975, Douglass 1977, Hohman et al. 1980) together record over 775 different publications concerning the genus, and more have been published since then. Compared to most other reptile species, an exceptional diversity of techniques has been employed, and many field methods have been developed and used to study their status and biology.

The gopher tortoise is a large terrestrial turtle (15-37 cm carapace length, 3.6-5.0 kg) that exhibits low rates of juvenile recruitment, extreme

adult longevity, and persistent use of a small number of burrows, often in a loose aggregation of 10 to 15 individuals. As a result, tortoises display a social system that involves individuals who may have interacted regularly for decades (Douglass 1976, Landers et al. 1980, McRae et al. 1980). Tortoises were once a common feature of the upland habitats of the southeastern coastal plain (Auffenberg and Franz 1982), but the species is now less common and appears on several state and federal lists of rare or endangered species (Lohoefer and Lohmeier 1984, Wood 1987). The principal forces driving these population declines are rapid urbanization, certain forest management practices, and human predation (Diemer 1986).

Gopher tortoise burrows are important to a large wildlife community, and 332 other species have been documented to use tortoise burrows at least occasionally (Jackson and Milstrey in press). Included among the several rare species that rely heavily on tortoise burrows are the Florida mouse (*Peromyscus floridanus*), Florida and dusky crawfish frogs (*Rana areolata aesopus* and *R. areolata sevosia*), sand skink (*Neoseps reynoldsi*), Florida pine snake (*Pituophis melanoleucus mugitus*), and eastern indigo snake (*Drymarchon corais couperi*).

In this paper we review techniques used in field research on the gopher tortoise community. We also discuss future areas of research and

Abstract.—This paper reviews methods used to census gopher tortoises as well as techniques for demographic, reproduction, and movement studies. We also evaluate a refinement for line transect estimates of gopher tortoise abundance. In situations where dense vegetation structure may hinder abilities to locate burrows along transects, Fourier series estimators of abundance can be used to overcome the problem. However, our results indicate that many transects may be needed to provide precise estimates of gopher tortoise abundance over large areas. The collection of vegetation data along transects may also be helpful in evaluating habitat preference in this species.

analyze the use of Fourier series estimators (Burnham et al. 1980) in line transect censusing techniques. In doing so we suggest appropriate methods for future work, standardize some techniques, bring some lesser known techniques to the fore, and suggest refinements to commonly used methods.

Estimating Population Size

Burrow Count Transects

Burrow-count transects are currently the most widely used method for estimating the size of local gopher tortoise populations, though some tortoise populations do not dig burrows (Auffenberg 1969), while others may use seven or more burrows per individual (McRae et al. 1980). Burrows are particularly amenable to transect analysis since they are stationary and generally visible in many of the open areas occupied by gopher tortoises. Transects also require little equipment, can be used to cover relatively large areas in a short time, and can be used to estimate abundance over a large area using random or stratified-random sampling procedures. A conversion factor (Auffenberg and Franz 1982) is used to relate the number of different tortoise burrows to the number of gopher tortoises in an area.

The dimensions of reported transects ranges from 100 to 250 m in

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length to 7 to 10 m in width (Auffenberg and Franz 1982, Cox et al. 1987, Lohoefer and Lohmeier unpub. rep.). Lohoefer (in press) points out that strip transect burrow counts assume that all burrows are detected within a strip. Breininger et al. (in press), however, expressed concern that dense vegetation could make strip-transect estimates unreliable unless the transects were narrow. The thick oak scrub (*Quercus* spp.) vegetation common on many of their study sites, for example, would have prohibited surveyors from seeing burrows more than a few meters from transect lines.

A possible method of correcting this problem (Cox et al. 1987, Lohoefer in press) is to take perpendicular distance measures from transect lines to observed gopher tortoise burrows. Perpendicular distances can be used in Fourier series density estimators (or other estimators) (Burnham et al. 1981) to account for differences in the detectability of burrows due to vegetation or the size of the burrow.

To look at this problem in more depth, we compared strip transects and line transects by establishing 12 transects (250 m by 20 m) in each of three areas containing gopher tortoise populations. The areas selected had noticeable differences in vegetative structure. The first site was a mixed longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) habitat on a private ranch; the second site was an early successional sand pine scrub (*P. clausa*) forest on private timber lands; and the third site was a mature longleaf pine forest in the Apalachicola National Forest. The starting points and directions of transects within these areas were randomly selected.

Perpendicular distances from burrows to transect lines were measured to the nearest 0.25 m, and only burrows detected from the transect line were recorded (i.e., burrows located while measuring perpendicular distances to burrows seen from the

transect line were ignored). Burrow densities for each of the three areas were estimated directly using the number recorded on transects and Fourier series estimators obtained from perpendicular distance data (table 1). Fourier series estimators were calculated using the TRANSECT program developed by Laake et al. (1979) and are presented in table 1 for the three sites.

Vegetation structure appeared to influence the estimate of burrow density on the early successional site (Site 2), but the Fourier series estimate of density was no different than the estimate provided by direct computations on the other sites. The early successional site had a very thick shrub component that made it difficult to locate burrows several meters from the transect line. Ten meters was probably too wide a transect width in this particular setting. The direct computation of burrow density from transect data on Site 2 is only half the density estimate developed by the Fourier series estimate.

The level of variation observed among transects (whether they be strip or line transects) within a site can be used to estimate the number of additional transects needed to attain a higher level of accuracy for the estimate of density (Burnham et al. 1981). To increase the precision of our estimates by 10%, for example, an additional 24 transects would be needed for Site 1, 40 for Site 2, and 78 for Site 3. Such an analysis can help determine whether additional surveys are needed, given the level of accuracy desired. For some questions, levels of accuracy of 20-30% may be acceptable.

Detecting small burrows of juvenile tortoises in transect sampling can be particularly difficult even in fairly open habitats (Douglass 1978). This problem weakens the reliability of transect data in estimating the abundance of juveniles. Fourier series estimators again could be used, in conjunction with an estimate of

burrow size, to gauge detectability of small burrows, but extremely large samples are probably needed to obtain an accurate detectability function and estimate of abundance for smaller tortoises.

Point-Center Burrow Counts

Tortoises often form small colonies of aggregated burrows (McRae et al. 1980), and H. Mushinsky and E. McCoy (Pers. comm., University of South Florida, Tampa, Florida) use a point-center method (Cottam and Curtis 1956) to estimate the size of tortoise colonies. The approximate center of the aggregation of burrows is estimated, and the center point of the census station is placed there. The distance from the center point to several tortoise burrows is determined, and a burrow density estimate is derived using standard point-center calculations (Cottam and Curtis 1956). If the abundance of tortoises over a large area is desired, all aggregations should be located.

Other Indirect Estimates of Density

In some situations (e.g., intensive colony analysis or preparation for population relocation), complete burrow counts are needed. We have used teams of 6 to 12 inexperienced field assistants, spaced at arm's length, to

Table 1.—Mean burrow density estimates (burrows per ha) and standard deviations calculated from transect data using Fourier series estimators (D) and direct computations. Data were collected at three sites in north Florida.

Location	Fourier series estimator (D)	Direct computations
Site 1	5.3 ± 0.957	5.5 ± 0.932
Site 2	7.9 ± 0.464	3.3 ± 1.351
Site 3	3.8 ± 0.799	3.8 ± 0.873

traverse an area and search intensively for burrows. Later searches by a more experienced researcher did not reveal any previously undiscovered burrows, except for a few cryptic hatchling burrows.

Trained dogs and aerial searches by helicopter (Humphrey et al. 1986) have also been used to locate gopher tortoise burrows. Gopher tortoises often defecate in or near their burrows, and a motivated dog can detect and locate the resulting olfactory source. Scats and carcasses are also important field sign used as indices of desert tortoise populations (Berry and Nicholson 1984, Woodman and Berry 1984).

Regularly used burrows often have several well-defined trails leading to foraging areas and other burrows (Ernst and Barbour 1972). We have used these trails to find burrows hidden in extremely dense vegetation.

Activity Patterns and Correction Factors for Burrow Counts

Although estimates of gopher tortoise burrow abundance are relatively easy to collect, calculating the

number of tortoises associated with those burrows can be difficult. It seems logical that the number of tortoise burrows would be positively correlated with the number of gopher tortoises in an area, but the precise nature of this relationship is poorly understood. Complicating factors include the level of human disturbance, soil type, and factors that influence gopher tortoise activity patterns (e.g., time of day, season, and weather conditions).

Most researchers have used a correction factor of 0.614 times the number of "active" and "inactive" burrows to estimate tortoises abundance from burrow counts. This conversion factor is based on information presented in Auffenberg and Franz (1982) that was derived from long-term data on the occupation rates of 122 burrows. Burrow activity was defined by Auffenberg and Franz (1982) in the following manner:

active (burrow) if the soil of the burrow had been recently disturbed by the tortoise, *inactive* if the soil were undisturbed but the burrow appeared to be maintained, and *old* if the mouth had been

washed in or covered with debris (1982:96) (*italics ours*).

Little experience is needed to learn to make these distinctions, but different investigators' classifications may vary, increasing the imprecision of tortoise abundance estimates. The precision is also affected by the activity level of tortoises. During warm periods tortoises may move among several burrows during a day; during cooler periods a tortoise may stay in a burrow for several weeks.

R. Stratton (Pers. comm.) suggests that it is possible to determine whether a burrow is occupied (i.e., active) by the direction of foot tracks on the burrow apron. Stratton was able to identify correctly 14 of 15 occupied burrows using this technique, but he incorrectly identified 19 unoccupied burrows as being occupied.

I. J. Stout (Pers. comm., University of Central Florida, Orlando Florida) has successfully used a "sewer snake" to determine if a burrow is occupied. When extended to the end of the burrow, the sound of the end of the wire tapping a tortoise shell is distinctive. Other methods include "feeling" for tortoises using long PVC pipes (Pers. comm., J. Diemer, Florida Game and Fresh Water Fish Commission Wildlife Research Laboratory, Gainesville, Florida) and listening for tortoises using either a flexible garden hose (Pers. comm., D.B. Means, Coastal Plains Institute, Tallahassee, Florida) or an electronic "ear" to amplify breathing sounds (Pers. comm., D. W. Speake, Alabama Cooperative Research Unit, Auburn, Alabama).

Several small twigs stuck vertically into the soil at the burrow mouth can also be used to determine if a burrow is occupied (Hallinan 1923, Beinger et al. in press). If properly spaced, one or more twigs will be knocked over the next time a tortoise passes. Direction of travel can be determined by uniquely marking the top of each twig (or using a "Y" shaped stick) and noting which di-

Table 2.—Examples of reported correction factors.

Tortoises/active burrow	Tortoises/inactive burrow	Tortoises/active+inactive	Source
•	•	n=122, 61.4%	Auffenberg and Franz (1982)
* 11%**	•	•	Breining et al. (in press)
49/103 (48%)**	•	•	•
33/103 (32%)**	•	•	•
67/124 (54%)	0/30 (0%)	67/154 (44%)	Burke (pers. obs.)
43/44 (98%)	3/16 (19%)	45/60 (75%)	Doonan (1986)
4/19 (21%)	0/25 (0%)	4/44 (9%)	Fucigna and Nickerson (in press)
35/174 (20%)	0/144 (0%)	35/318 (11%)	•
•	•	127/411 (31%)	Linley (1986)
* 61.5%	•	•	Lohoefer (1982)
9/19 (47%)	0/225 (0%)	9/244 (4%)	Speake (1983)
7/10 (70%)	0/47 (0%)	7/57 (12%)	•
* 66.0%	•	•	Spillers and Speake (1986)
•	•	10/89 (11%)***	Stout et al. (in press)

*Not reported or additional details not reported.

**Includes "maybe active" activity classification.

***Unknown number of tortoises had been harvested prior to survey.

rection the twig falls. The twigs can be resurveyed 1-3 days after placement.

Some recent studies involving total colony capture (Doonan 1986, Stout et al. in press, Fucigna and Nickerson in press, Linley 1986, R.L. Burke unpublished data), using a miniature underground television camera (Burke pers. obs., Breininger et al. in press, Spillers and Speake 1986) or other techniques have provided reliable determinations of the number of tortoises per burrow. These studies (table 2) have reported a wide variation in the appropriate correction factor, from 4% of active and inactive burrows (Speake 1983?) to 75% (Doonan 1986).

Breininger et al. (in press) suggest that an appropriate correction factor must be determined on a case-by-case basis. They recommended that at least 20 active and inactive burrows be surveyed by other methods (e.g., by camera techniques, trapping, or by stick placement at the mouth of the burrow) to establish an accurate correction factor for a site.

Capture Techniques

Gopher tortoises spend most of their time in burrows (McRae et al. 1980), which makes it difficult to observe or capture animals above ground. It is not known how much time gopher tortoises spend in above ground activities, but the congener desert tortoise is inactive for about 98% of its life (Nagy and Medica 1986).

Once inhabited burrows are located, tortoises may be captured and counted directly by any of several methods. The methods vary in terms of time and resource expenditures required and the degree to which habitat conditions are disturbed.

Trapping

Many researchers use a version of bucket trapping similar to that origi-

nally reported by Agassiz (1857). This fairly non-disruptive technique involves burying a smooth sided plastic bucket (usually a five-gallon size) immediately in front of the burrow, and covering the trap loosely with a cloth or a sheet of heavy paper. The trap is then disguised with a thin layer of soil.

Drainage holes may be drilled in the bottom and sides to prevent accumulation of rainwater, which can drown a captured tortoise. However, in extremely hydric soils, traps should not have holes because water entering from the ground can cause the same problem.

In general, traplines should be closed down during periods of heavy rains. Traps should be checked at least daily, and during very hot weather there is a risk of overheating and killing captured animals (Burke 1987, Taylor 1982). It may help to shade exposed traps. Smaller cans and containers may be used for capturing juvenile and subadult tortoises.

Bucket trapping is labor intensive, but once traps are in place they are easy to monitor. Up to forty traps may be installed by an experienced person per day, and over 100 traps can be checked and reset if necessary per person per day. We found that over 90% of bucket-trapped tortoises were captured in the first 21 days, suggesting that three to four weeks is required to capture nearly all tortoises.

These results are very similar to the results obtained by J. Diemer (Pers. comm., Florida Game and Fresh Water Fish Commission Wildlife Research Laboratory, Gainesville, Florida). An absence of signs of above-ground activity after placement of traps helps to indicate whether all occupied burrows in the area have been located and trapped.

Martin and Layne (1987) placed standard live mammal traps at the entrance of the burrow to capture tortoises. Snares have also been used by Novotny (1986) and ourselves

with some success. They may be set so as to catch the leg of the tortoise and therefore limit possible injury, though Taylor (1982) describes the use of snares to kill pest tortoises. Although snares are inexpensive and easy to set, they are easily evaded and may occasionally injure a noosed animal.

Auffenberg (in Plummer 1979) and Recht (1981) described using mechanical and electronic burrow-excluding devices to force tortoises to remain above ground after leaving their burrows. Recht (1981) pointed out that, if such a mechanism was equipped with transmitting apparatus, the tortoise could be captured immediately.

Deception

"Handbobbing" (Burke 1987, Linley 1986) may entice tortoises to emerge from burrows, apparently by eliciting a territorial response. This technique involves bobbing a clenched fist in short, jerky motions at the mouth of the burrow, which is similar to the head bobbing that tortoise engage in as part of social interactions (Auffenberg 1969). Once a territorial response is initiated, tortoises will attempt to push the intruding hand from the burrow and can be maneuvered into a position to be extracted. Success may be enhanced by striking the ground several times before handbobbing and by tossing a small amount of soil down the burrow. Mirrors can also elicit a territorial response (Legler and Webb 1961).

A somewhat similar technique, "tapping," has been used to capture desert tortoises (Medica et al. 1986). Tapping involves lightly rapping on the tortoise's shell with a long stick. This procedure would be difficult to employ successfully where burrows are long and curved. We have used sewer snakes to probe for tortoises at the end of their burrows, but we have not elicited a response by shell tapping.

Burrow Excavation and Pulling

Digging up the entire burrow with a backhoe or hand shovel is both time consuming and destructive. At one South Florida site, it took an experienced backhoe operator 2.5 hours to excavate one burrow that was over 11 m long and 6 m deep. Most burrows are excavated in less than 45 minutes using a backhoe, which compares favorably to the approximately 30 days of bucket trapping required to remove all tortoises from an area (Diemer et al. in press).

When excavating a burrow, a sewer snake or garden hose should be extended to the end of the burrow to keep track of the tunnel path. The entire process is complicated by loose, sandy soils at some sites, and it is difficult to retain burrow structure and avoid potentially dangerous cave-ins. The difficulty of the process may be reduced by using an electronic device to locate the burrow end before digging (see Wolcott 1981). Small commensal species are likely to be buried when a burrow is excavated mechanically, but excavation by hand is extremely labor-intensive (Ernst and Barbour 1972).

Taylor (1982) describes the history of a pulling "hook" first reported by Fisher (1917). It is the only simple, quick, and moderately reliable method for capturing tortoises, used principally by tortoise hunters. Pulling requires the use of a long flexible rod attached to a short stout piece of bent wire. The apparatus is fed into the burrow, maneuvered behind the tortoise, and wedged between the rear of the plastron and the flared carapace. Success rate is influenced by a puller's skill and by the length and curvature of the burrow. In regions that have been heavily "pulled" in the past, remaining tortoises are most often found in winding burrows that are particularly difficult to pull (R. Stratton, Pers. comm.). Taylor (1982) gives details on the procedure, as well as statistics on the damage to captured tortoises.

Techniques for Studying Tortoise Demography and Reproduction

Estimates of Population Structure Using Burrow Width

Alford (1980) and Martin and Layne (1987) have demonstrated that a simple mathematical relationship exists between the width of a burrow and the size of the resident tortoise. Thus, on the basis of a burrow census, burrow widths, and a reliable correction factor, it is possible to estimate population size and evaluate demographic structure (Alford 1980, Sauer and Slade 1987). The relationship between burrow width and size of occupant may be slightly biased, however, since small tortoises can occupy large burrows but the obverse is impossible.

Marking Techniques and Determining Sex and Age

Marking tortoise shells is an easy way to follow the fate of individuals over long periods of time. Techniques for marking marginal scutes of turtles have been reviewed by Ferner (1979) and Plummer (1979).

Based on variation in the shell dimensions of 183 adult tortoises of known sex, McRae et al. (1981) developed a discriminate equation that can be used to determine accurately the sex of adult tortoises from north Florida and south Georgia. The applicability of the technique to tortoises from other areas, and to smaller size classes, is untested (Wester 1986).

Graham (1979) reviews four age-determination techniques: mark/recapture, records of captive specimens, examination of long bone sections, and scute ring counts. Of these, only scute ring counts have been reported for gopher tortoises. W. Auffenberg (Pers. comm., Florida State Museum, Gainesville, Florida) suggested that a pencil rubbing of the plastron was an accurate way

both to record true scute rings and to avoid counting false rings. This has been confirmed by L. Landers (unpub. data, Tall Timbers Research Station, Tallahassee, Florida). Additional methods of counting and recording scute rings are given by Galbraith and Brooks (1987).

Landers et al. (1982) demonstrated that, in southern Georgia, age can be accurately estimated by carefully counting plastron scute rings. Germano and Fritts (in press) used mark/recapture data to show a high correlation between age and scute ring counts of 17 known-age desert tortoises (less than 25 years old) from Nevada. They propose microscopic examination of thin scute sections can help determine age of older tortoises. However, Berry (in press) presents data from 190 desert tortoises from 11 study sites in which scute rings were not annual. Ring deposition varied from 0 to 3 rings per year. Berry and Woodman (1984) discuss the use of shell wear classes for age determination of adult desert tortoises.

Studies of Tortoise Reproduction

Indirect indications of reproductive activity include swelling of the subventral glands and recent evidence of gravidity. Auffenberg (1966) and Rose (1970) suggested that the subventral glands produce pheromones important to courtship and mating behavior, and Landers et al. (1980) used the swollen condition of these glands in some captured tortoises as an index to sexual activity.

Although the clutch size of gravid tortoises can be determined by radiography (Turner et al. 1986), field methods are limited to palpation and weight loss. T. Linley (Pers. comm.) uses palpation to estimate clutch sizes for gravid females with well calcified eggs. Turner et al. (1986) also regularly weighed transmittered desert tortoises and used sudden weight loss to indicate oviposition.

Given the fairly predictable nature of tortoise nest location (Hallinan 1923), it is surprising that so few field data have been collected on nest predation, nest microclimate, sex of offspring, time of emergence, etc. Auffenberg and Iverson (1979) in north Florida, and Landers et al. (1980) in south Georgia, provide estimates of predation rates and nest viability, but more information is needed to construct accurate estimates of nesting success over time, one of the more critical portions of tortoise life cycles (Diemer 1984). Marshall (1987) and Douglass and Winegarner (1977) also report preliminary studies on nest predation using sign at a small number of regularly visited nests.

Camera traps may be particularly useful in egg predation studies, allowing precise identification of timing and predator. R.L. Burke and M. Noss (pers. obs.) attempted to detect soil disturbance due to egg laying by burying a layer of colored gravel in 46 burrow mounds before oviposition season. No activity was detected, however. Careful use of an egg probe (Hallinan 1923) may facilitate rapid searching of large numbers of burrow mounds for egg clutches.

Movement Studies

In addition to studies employing direct observation and capture-recapture techniques (e.g., Auffenberg and Iverson 1979, Douglass and Layne 1978, McRae et al. 1980, Landers et al. 1980), various remote sensing devices have been used to monitor tortoise movements.

String trailers (see Ferner 1979 and Plummer 1979) have been used for daily movement and path length studies (Pers. comm., W. Auffenberg, Florida State Museum, Gainesville, Fl., McRae et al. 1980). Tortoises too small for radio transmitters may be tracked using a metal detector to locate small pieces of different metals attached to their shells.

Radio telemetry (Legler 1979) of gopher tortoises has been used by Burke (1987), Fucigna and Nickerson (in press), McRae et al. (1980), Stout et al. (in press), J. Diemer (unpublished data, Florida Game and Fresh Water Fish Commission Wildlife Research Laboratory, Gainesville, Florida) and others. Radios are attached to anterior of the carapace on females (to avoid interference with copulation) and either the anterior or posterior of males. Dental acrylic is typically used to fix the transmitter on the shell, and the entire device is covered in silicone sealant for additional protection. Other researchers (e.g., Stout et al. in press) have used machine screws or wire to attach the radio to the shell. Antennae are usually glued along the shell or left dragging.

Auffenberg and Iverson (1979) used a series of microswitches and sensors buried along, and extending into, numerous tortoise burrows to correlate inner-burrow movements with microhabitat environmental conditions.

Commensal Studies

General methods for trapping reptile and amphibian species are reviewed by Campbell and Christman (1982) and Vogt and Hine (1982). Crawfish frogs may be seen at night sitting in the mouth of the burrow (Hallinan 1923), and are sometimes captured in bucket traps, small mammal traps, and funnel traps set for other species (Franz 1986). General marking techniques for reptiles and amphibians are reviewed by Ferner (1979).

Day et al. (1980) give a general review of capture and marking techniques for mammals, birds and reptiles, and Mengak and Guynn (1987) compare different trapping methods for small mammals and herpetofauna. Eisenberg (1983) describes successful placement of traps for Florida mice. As described above, digging up the burrow by hand is the only known way reliably to capture

all burrow commensals, especially invertebrates. W. Auffenberg (Pers. comm., Florida State Museum, Gainesville, Florida) and Milstrey (1986) have used vacuum systems to sample invertebrates in burrows. Milstrey (1986) and Woodruff and Klein (in prep.) also describe various small, baited pitfall traps for capturing invertebrates. Butler et al. (1984) describes a CO₂ trap that is useful for collecting ticks and fleas.

Vegetation Analysis

A small number of researchers has attempted to characterize gopher tortoise habitat using quantitative methods. Breininger et al. (in press), Marshall (1987), and Wester (1986) related gopher tortoise densities to vegetation structure, while Auffenberg and Iverson (1979) analyzed the relationship between tortoise densities and a single vegetative component, herbaceous ground cover. Quantitative vegetation sampling has become a standard element in survey techniques used for other groups (e.g., breeding bird censuses, James and Shugart 1970), and these techniques should be more widely applied to tortoise research.

We collected vegetation data at 50 m points as part of the transect study described above. Percent canopy cover (trees > 5 m), percent shrub cover, percent ground cover, percent wiregrass (*Aristida stricta*) cover, and the relative percent of deciduous trees to coniferous trees were measured using methods described in Cox et al. (1987). These five variables were selected based on published information about gopher tortoise habitat preferences (Campbell and Christman 1982, Diemer 1986), but several other variables could also be considered.

A principal components analysis was performed on the vegetation data using a "varimax" rotation procedure (Wilkinson 1980). The density (per ha) of active and inactive gopher

tortoise burrows along each of the 32 transect segments was then plotted against the transect's vegetation score on the first principal component axis. This procedure helps gauge the degree to which variation in tortoise density along transects

Table 3.—Factor loadings for 6 habitat variables measured along transects. Weightings and contrasts were derived from a "varimax" principal component (PC) analysis (Wilkinson 1983).

Variable	PC 1	PC 2
Canopy cover	0.809	-0.278
Shrub cover	-0.896	0.171
Ground cover	-0.832	0.044
Deciduous/coniferous overstory	0.090	0.900
Percent wiregrass	0.607	0.550
Percent variance explained by axis	50.5%	24.4%

relates to variation in vegetation structure. The average values for vegetative samples recorded along transects was used to compute principal component scores. Too few samples were collected to produce a very precise evaluation between burrow density and vegetation structure, so the effort should be considered only as an example of the application of vegetation data collected along transects.

Principal component analysis of vegetation data accurately projected the differences we casually observed among sites. The first principal component axis explained 50.5% of the variation among samples and largely contrasted decreasing canopy cover and wiregrass percentages with increasing shrub and ground cover (table 3). High positive scores along this axis indicate decreasing percentages of canopy cover and wiregrass, increasing amounts of shrub cover

and ground cover, and increasing ratios of deciduous to coniferous trees. The second principal component axis explained an additional 24.4% of the sample variance and is weighted by decreasing amounts of wiregrass cover and the ratio of deciduous to coniferous trees (table 3).

A plot of burrow densities against the first principal component shows a general trend of increasing burrow density with decreasing principal component value (fig. 1). Areas with greater burrow densities generally had a lower percentage of canopy cover, but higher percentages of shrub and ground cover, than areas with lower densities. The regression line drawn through the points has an adjusted r^2 of 0.37 ($p < 0.05$).

Future Directions

Burrow-count transects are efficient for estimating burrow density, but they may not produce sufficiently accurate estimates of gopher tortoise densities. The relationship between burrow density and tortoise density is poorly understood, and studies analyzing the relationship between burrow occupancy and burrow activity class are needed to strengthen abundance estimates. Whether transects are appropriate will depend on the questions being addressed.

The combined effects of variation in occupancy rates and variation in burrow counts among transects may easily produce estimates of tortoise abundance that span an order of magnitude. For example, a 95-confidence interval for the density of active and inactive burrows on our second study area (using the Fourier series estimate from table 1) is 3.326-12.55 burrows per ha. If the occupancy rate of 20 active and inactive burrows was followed for a week on this site and determined to be 0.60 ± 0.20 for any one day, then a 95-confidence interval for the estimated density of tortoises on the site could range from 0.69 to 12.4 tortoise per

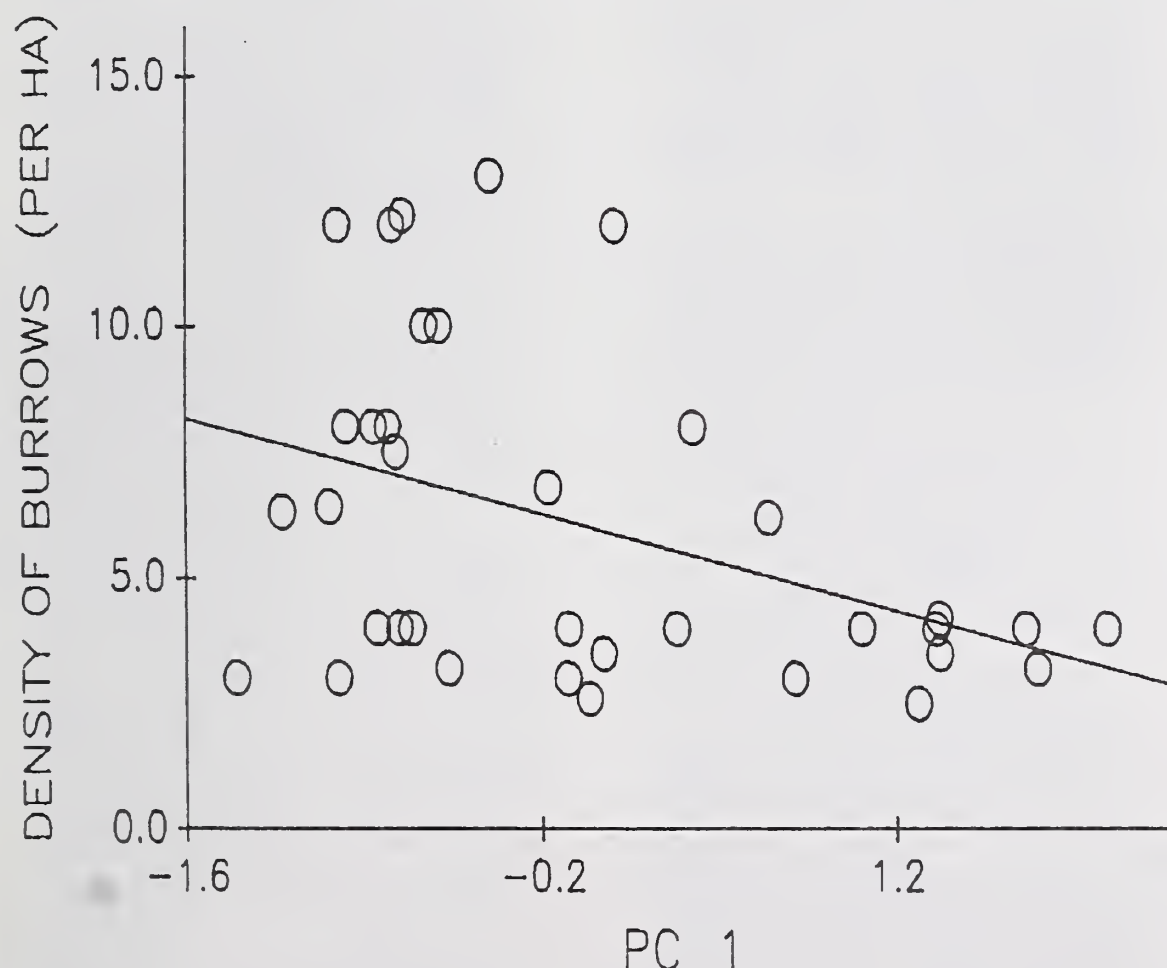


Figure 1.—Gopher tortoise burrow density estimates plotted along first principal component axis. High positive scores along PC1 have low canopy cover and relatively high levels of herbaceous ground cover and shrubs.

ha. Clearly this is too large a range for some, if not most, ecological questions. Many more transects and more precise occupancy rates would be needed to correct these problems.

Fourier series estimators should be used when transects are conducted in areas with a dense shrub component. Some strip-transect estimates of gopher tortoise densities in thick, scrubby areas may have underestimated density. Indeed, Breininger et al. (in press) found high tortoise densities on areas with thick shrub levels that traditionally might not have been considered appropriate gopher tortoise habitat.

Repeated samples of burrow activity over time should be used to estimate site-specific correction factors, rather than rely on a single generalized correction factor. This can be easily done, requiring only a return visit to 20 or more randomly chosen burrows. As such data accumulate, they may lead to a more appropriate correction factor.

Additional studies of the commensal community are also needed since very little is known of the interactions that occur among commensal species. Certain mutualistic relationships may be critical to the survival of many of these species and be important in efforts to relocate components of the burrow community (e.g., Diemer et al. in press). Video camera techniques (Breininger et al. in press, Spillers and Speake 1986) offer a great potential for investigating burrow ecology.

Additional studies of the early life cycles of gopher tortoises may also be worth pursuing, particularly in terms of conducting management for this species. The critical survival period in the gopher tortoise life cycle occurs during the first few years of life (Diemer 1984). If nesting success and hatchling survival can be effectively manipulated through management activities, such activities would need to be conducted fairly infrequently to enhance population size over many years.

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Talus Use by Amphibians and Reptiles in the Pacific Northwest¹

Robert E. Herrington²

In recent years, biologists have emphasized the importance of preserving habitats with high species diversity (Ehrlich and Ehrlich 1981). In this context, habitats that play a critical role in the life cycle of a large number of species should also be considered for protection. However, there is little information available concerning habitat utilization by many amphibian and reptile species, and even less on the combined use of a single habitat by both of these groups (but see Scott and Campbell 1982).

Obtaining data on habitat use of amphibians and reptiles is often hindered by the fact that habitat fidelity is extremely variable for these groups. Most studies have concerned eastern species, but some generalizations have emerged. Small species may be more or less restricted to a single habitat (Ashton 1975, Barbour et al. 1969, Fitch 1958, Gregory et al. 1987, and Rose 1982). Others routinely occupy two or more distinctly different habitats over a single season. The latter group includes species that migrate to reproduce and those which use a separate habitat for hibernation and/or aestivation (Brown and Parker 1976, Duvall et al. 1985).

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Abstract.—Field data and a review of available literature were used to categorize the extent of talus usage by individual herpetofaunal species. Five categories were recognized that ranged from species essentially restricted to talus slopes to those that were only occasionally observed there. More than 60% of the amphibian and reptile species that occur in the states of Oregon and Washington were found to utilize talus habitats. In addition to species essentially restricted to talus slopes, the most frequent use patterns were to moderate the effects of adverse seasonal weather conditions and the use of talus slopes for reproductive activities.

However, the importance of a habitat to the continued survival of a population is not necessarily correlated with the time that a species spends within it. Providing reproductive habitat, refugia from adverse weather conditions, or protection from predators can disproportionately influence the role that a particular habitat plays in the ecology of the animals that use it.

Talus slopes are "unique habitats" (Maser et al. 1979), that represent the gradual accumulation of weathered rock fragments (mostly basalt and andesite) from a cliff face (Strahler 1981). Individual slopes are quite variable in rock size, aspect and in the amount and type of vegetation present. These factors interact in complex ways to provide a broad range of thermal and moisture regimes that amphibians and reptiles can select. This study examines the use of talus slopes by amphibians and reptiles and compares these findings with non-talus areas.

Study Area and Methods

Herpetofauna associated with talus slopes and adjacent non-talus areas was determined by field observation and a review of the literature (Campbell et al. 1982). For the purpose of this investigation, talus habitats were those in which the substrate was predominantly weathered rock fragments (typically with an as-

sociated cliff-face) and included a 10 meter wide band of transitional habitat. Non-talus habitats were those in which the substrate was not as described above and were located a minimum of 100 meters from a talus area. Aquatic habitats were not specifically sampled; however, specimens observed under objects located above the high water mark were included in the analysis.

Field work was conducted between August, 1981 and August, 1985. During this period, more than 100 days were spent in the Cascade Mountains of southern Washington and northern Oregon. Additional surveys ranging from 2-6 days each, were conducted in the North Cascades of Washington, the Coast Range of southern Oregon, and the Wallowa Mountains of northeastern Oregon. A total of 183 individual talus slopes and adjacent non-talus areas were surveyed. Approximately equal time was spent searching talus and adjacent non-talus habitats. Talus slopes were considered to have been altered by human activities if there was evidence of extensive rock or tree removal.

Searches were conducted by turning surface debris, raking through leaf litter, and in the case of talus, by digging in the upper layers of rock with a potato rake. Data recorded for most specimens included habitat type, the activity the animal was engaged in when first observed (active or inactive, surface or sub-surface,

Table 1.—Talus use by amphibians and reptiles observed during this study. Use patterns by individual species were: (1) species generally restricted to Talus habitats; (2) species which use talus areas for reproductive activities; (3) species which use talus areas to survive adverse weather conditions; (4) species frequently associated with talus areas; (5) species occasionally observed in talus habitats.

Species	Talus/non-talus habitats	Numbers of individuals observed in
		talus use pattern(s)
AMPHIBIANS		
Frogs		
<i>Hyla regilla</i>	3/21	3
<i>Rana aurora</i>	2/17	3
<i>Rana cascade</i>	0/6	—
<i>Rana pretiosa</i>	0/17	—
<i>Bufo boreas</i>	2/9	5
<i>Ascaphus truei</i>	2/18	5
Salamanders		
<i>Ambystoma gracile</i>	3/8	3
<i>Ambystoma macrodactylum</i>	5/63	3
<i>Dicamptodon ensatus</i>	8/5	2,3
<i>Rhyacotriton olympicus</i>	26/109	3
<i>Aneides ferreus</i>	3/8	5
<i>Plethodon elongatus</i>	43/3	1
<i>Plethodon dunni</i>	123/87	3,4
<i>Plethodon larselli</i>	383/20	1,2,3
<i>Plethodon vehiculum</i>	193/146	2,3,4
<i>Plethodon vandykei</i>	31/3	1
<i>Plethodon stormi</i>	19/0	1
<i>Ensatina eschscholtzi</i>	32/26	4,5
<i>Batrachoseps wrighti</i>	13/8	4,5
<i>Taricha granulosa</i>	5/32	3
REPTILES		
Lizards		
<i>Elgaria coerulea</i>	19/9	3,4
<i>Elgaria multicarinata</i>	3/0	2,3,4
<i>Eumeces skiltonianus</i>	5/3	4
Snakes		
<i>Contia tenuis</i>	2/0	3,4
<i>Coluber constrictor</i>	10/21	3
<i>Charina bottae</i>	4/2	4
<i>Diadophis punctatus</i>	2/2	4
<i>Hypsiglena torquata</i>	2/0	3,4
<i>Pituophis melanoleucus</i>	8/5	2,3
<i>Thamnophis elegans</i>	9/11	3
<i>Thamnophis ordinoides</i>	16/3	2,3
<i>Thamnophis sirtalis</i>	13/19	2,3
<i>Crotalus viridis</i>	28/5	2,3
NUMBER OF INDIVIDUALS	1017/686	
SPECIES RICHNESS	31/29	

foraging or involved in reproductive activities), and a subjective evaluation of the individual's approximate age (hatchling, juvenile, or adult). The determination that an individual was using talus to avoid unfavorable weather conditions was based on the season, prevailing weather conditions, the behavior exhibited by the animal when uncovered, and the depth at which the specimen was located.

These observations were summarized in an effort to categorize patterns of talus use. Voucher specimens of most species have been deposited in the vertebrate collection, Department of Zoology, Washington State University. However, the majority of specimens were identified in the field and released at the site of capture.

Results and Discussion

Habitat Use

A total of four species of frogs were observed in talus habitats (table 1), with a fifth species reported using talus areas for feeding (table 2). A single *Hyla regilla* and two *Rana aurora* were located under snow covered talus and were considered to have been hibernating there. All frog species were more numerous in non-talus areas and two species (*Rana cascade* and *R. aurora*) observed in non-talus areas were not recorded from talus areas.

Salamanders were numerically and taxonomically the most abundant amphibians encountered during the study. The number of species recorded from talus and non-talus habitats were 14 and 13, respectively (table 1). However, species richness is somewhat misleading, since more than 90% of the observations of *Plethodon elongatus*, *P. larselli*, *P. stormi*, and *P. vandykei* were from talus habitats. I consider these species to be essentially restricted to forested talus areas. This observation is supported by the work of Stebbins and Rey-

nolds (1947) with *P. elongatus*, Nussbaum et al. (1983) with *P. stormi* and *P. vandykei*, and Herrington and Larsen (1985) with *P. larselli*. Five additional species (*Dicamptodon ensatus*, *P. dunni*, *P. vehiculum*, *Ensatina eschscholtzi*, and *Batrachoseps wrighti*) were observed more frequently in talus than in other habitats (table 1).

All the salamanders mentioned above with the exception of *Dicamptodon ensatus*, are capable of completing their entire life cycle within talus habitats. I observed portions of the courtship sequences of *Plethodon vehiculum* and *P. vandykei* only on damp talus. Many of these same species probably nest in deep recesses within the talus. This is based on two observations. The first is that given the abundance of some salamander species, very few nests have ever been located (Hanlin et al. 1979, Jones and Aubry 1985). This suggests that nests are located in places generally inaccessible to investigators. The slope and rock size associated with talus fields generally precludes digging at depths > 50cm without the talus caving in. Secondly, I found small aggregations (1-3 individuals) of *P. larselli*, *P. vehiculum*, and *P. dunni*, that approached the size reported for hatchlings (Stebbins 1951, Peacock and Nussbaum 1973, Herrington 1985) only in loose talus areas, following the first fall rains. This is the time that recent hatchlings are likely to emerge from their nests.

Individuals uncovered from talus in situations suggesting that they were in winter dormancy included *Ambystoma gracile*, *A. macrodactylum*, *Dicamptodon ensatus*, *Rhyacotriton olympicus*, *Plethodon dunni*, *P. larselli*, *P. vehiculum*, and *Taricha granulosa*. Conversely, between June and August there was reduced rainfall and elevated surface temperatures throughout most of the study areas. Because of this, surface activity by salamanders was greatly restricted and the majority of observations (83%) were of individuals uncovered from talus areas.

A total of 5 species of lizards were observed or reported from talus habitats (tables 1 and 2). *Elgaria coerula* was the most frequently observed species and most individuals were uncovered from the upper layers of talus. Two behavioral patterns were apparent. The first involved individuals uncovered before they had emerged from nocturnal retreats and the second was of individuals thermoregulating under surface talus. *Elgaria coerula* is a live-bearing species and this behavior may be important to the developmental processes taking place. Talus habitats have been identified as oviposition sites for *Sceloporus occidentalis* and *Uta stansburiana* (Maser et al. 1979) and *Elgaria multicarinata* (Brodie et al. 1969). *Elgaria coerula* and *E. multicarinata* were uncovered from talus slopes where they appeared to be hibernating.

Ten species of snakes were observed (table 1) and two additional species reported from talus habitats (table 2). Taken as group, snakes were most frequently observed basking either on the surface or between exposed rocks. Species that I considered to be entering or emerging from

hibernacula located within talus were *Crotalus viridis*, *Pituophis melanoleucus*, *Coluber constrictor*, *Thamnophis elegans*, *T. ordinoides*, *T. sirtalis*, *Hypsiglena torquata*, and *Contia tenuis*. Both *Hypsiglena torquata* and *Contia tenuis* were only observed in talus habitats during the study, but they are known to occupy a broader range of habitats elsewhere (Cook 1960; Diller and Wallace 1981).

Talus slopes play an important role in the reproductive activities of snakes. Brodie et al. (1969) reported several individuals of *Coluber constrictor*, *Diadophis punctatus*, *Contia tenuis* and *Pituophis melanoleucus* ovipositing within an exposed talus slope in Benton Co., Oregon. I observed gravid females of *Thamnophis sirtalis*, *T. ordinoides* and *Crotalus viridis* basking on talus slopes during late summer. Whether these snakes delivered their young at the talus slopes is not known. However, gravid *C. viridis* are known to remain in the vicinity of their hibernacula to produce young (R. Wallace, Department of Biological Sciences, University of Idaho, pers. comm.), and I uncovered 7 "yearling" *T. ordinoides* from an area of talus less than 2 m²,

Table 2.—Amphibian and reptile species not observed during this study, but which have been reported to utilize talus habitats. The categories of talus use are described in table 1.

Species	Talus use pattern	Reference
AMPHIBIANS		
Frogs		
<i>Bufo woodhousei</i>	5	Maser et al. (1979)
REPTILES		
Lizards		
<i>Crotaphytus bicinctores</i>	4	Nussbaum et al. (1983)
<i>Sceloporus occidentalis</i>	2	Maser et al. (1979)
<i>Uta stansburiana</i>	2	Maser et al. (1983)
Snakes		
<i>Lampropeltis zonata</i>	1	Nussbaum et al. (1983)
<i>Masticophis taeniatus</i>	2	Nussbaum et al. (1983)

where they appeared to be in hibernation. It was not possible to determine if these snakes had independently congregated there, or if they represented a single litter born at the talus slope, but the latter explanation seems more plausible.

The importance of talus slopes in the feeding ecology of snakes is unknown. The relative abundance of garter snakes and salamanders on talus slopes at certain times of the

year could lead to predator-prey interactions. This is supported by evidence palpated from the stomachs of two *Thamnophis sirtalis* and one *T. ordinoides* captured on talus slopes. Each of the *T. sirtalis* contained a salamander (1 *Plethodon dunni*; 1 *Ensatina eschscholtzi*); the single *T. ordinoides* contained a large slug (*Ariolimax* sp.). While other interactions were not observed, small mammals often were observed in talus habitats.

Alterations to Talus Slopes

It became apparent after the initiation of this study, that a large number of the talus slopes being surveyed had been or were being altered by human activities. Habitat modifications involved two not mutually exclusive alterations. The first was the removal of rock from the base of talus slopes to be used for road construction raw materials (fig. 1). The second involved tree removal (clearcutting) from the talus slopes.

I revisited talus slopes surveyed in the early part of the project to determine the frequency and type of alteration. Of 183 talus slopes surveyed, 106 were altered; 76 had noticeable quantities of talus removed, 13 had been deforested, and 17 had been altered by both events.

I was able to document few clear species specific trends between altered and unaltered talus slopes (see Conclusions). However, there were differences in the number of individuals encountered. Unaltered slopes represented 42% of the habitats surveyed but yielded 73% of the total number of individuals. Because there were differences in the amount of search effort (time) expended surveying altered and unaltered talus habitats, I did not statistically compare these results.

Conclusions

Talus slopes provide important habitat for a significant segment of the herpetofauna of the Pacific Northwest. A total 37 of the 58 species of amphibians and reptiles that occur in the states of Washington and Oregon are documented from talus slopes. Use of this resource by amphibians and reptiles was quite variable, but three important patterns emerged. The first involves species essentially restricted to talus habitats. Four species of plethodontid salamanders fit this pattern (*Plethodon larselli*, *P. vandykei*, *P. elongatus*, and *P. stormi*).

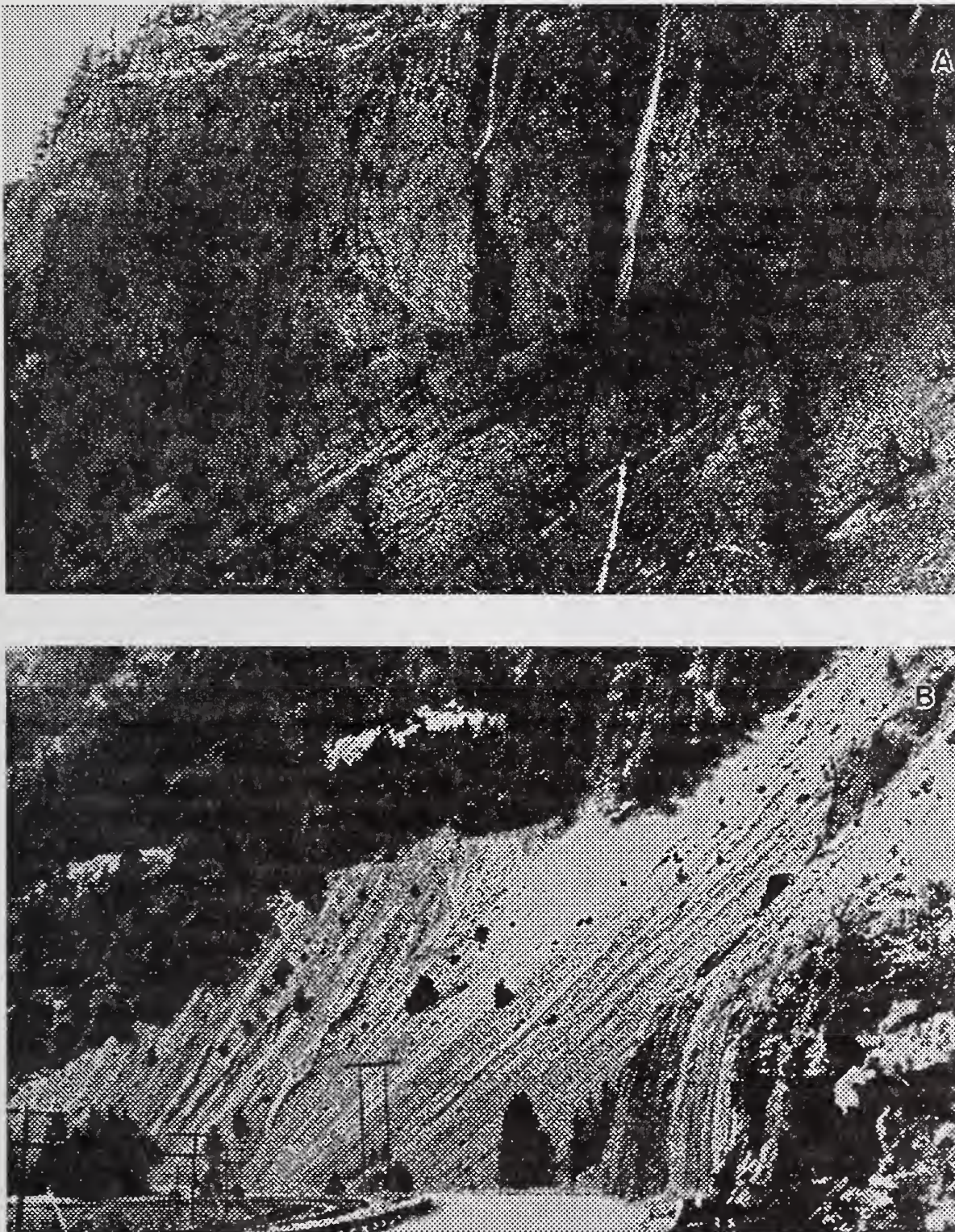


Figure 1. A comparison between the structure of an unaltered talus slope in winter (A) and a slope that has had extensive rock removal for road building raw materials (B).

The second category of talus use consisted of species which use talus slopes to avoid potentially lethal temperature extremes. Nineteen species (10 reptiles, 9 amphibians) were included here. Several species of snakes travel considerable distances to congregate at communal hibernacula (Duvall et al. 1985, Gregory and Stewart 1975, and Brown and Parker 1976). This behavior conceivably could put an entire population at risk if the hibernacula were irreparably altered.

A third use pattern of talus slopes was for reproductive activities. In addition to an egg-laying aggregation of 5 species of reptiles reported by Brodie et al. (1969), live-bearing reptiles were frequently observed in thermoregulatory behaviors on and along the edge of talus slopes. The importance in this behavior to completion of developmental processes remains to be determined.

Each of these utilization patterns is important to a particular segment of the herpetofaunal community. Whether or not the availability of suitable talus slopes is a limiting factor for any of these species remains unknown. However, talus slopes typically make up only a small portion of the available habitat. In the Gifford Pinchot National Forest (where a large part of this work was conducted), Scharpf and Dobler (1985) found talus slopes to occupy less than 5% of the total land area, most other areas have less.

The high frequency of altered talus slopes observed during this study may pose a significant threat to the long-term survival of many of the amphibians and reptiles that use them. Talus removal for road building materials and tree removal from the slopes initiate complex changes in the structure of the slope. Trees, through leaf fall, provide a major input of nutrients to the slope, as well as increasing the moisture retention capabilities of the sub-surface talus. Tree removal increases the solar radiation reaching the slope and this

results in the rapid loss of moisture from the upper layers of talus. In a study comparing the habitat selection of *P. larselli* and *P. vehiculum* (Herrington and Larsen 1985), tree removal was implicated in rendering a talus slope unsuitable for habitation by *P. larselli*, but not for *P. vehiculum*.

Talus removal results in a major shift of the slope towards its base. This results in the extensive movement of both surface and deep layers of talus. The immediate effect would be to kill or injure many of the reptiles and amphibians inhabiting the slope as well as destroy any nests located there. A long term consequence of rock removal is that erosional processes are increased. This results in an increase in the amount of soil present in the talus, and could conceivably close off access and fill in areas formerly used as hibernacula.

Management Recommendations

Prior to altering a particular talus slope, a survey should be conducted to determine the presence of threatened, endangered, or otherwise sensitive species. Additionally, it should be determined whether or not the slope in question serves as a major snake hibernaculum.

Tree removal from talus slopes should be restricted and logging practices should be modified to allow for leaving a sufficient border of trees (20-30 m) along the margin of talus slopes.

Current practices of removing talus for road building materials from each slope encountered should be discouraged. Selected talus areas known not to contain threatened, endangered or sensitive species or to be major snake hibernacula should be utilized as a source of rock for construction activities.

One area that needs additional study is the colonization and use by amphibians and reptiles of artificially created talus areas. These would include areas such as the banks of road

cuts with riprap, and rock piles associated mining processes. Those sampled during the study were found to have a depauperate fauna compared to natural talus areas and the fauna consisted almost entirely of species known to have broad habitat tolerances. However, the possibility remains that with adequate planning, suitable areas could be constructed in such a manner to benefit amphibians and reptile faunas.

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Comparison of Herpetofaunas of a Natural and Altered Riparian Ecosystem¹

K. Bruce Jones²

Over the past 25 years, concerns have increased about the impacts of population growth and associated development on wildlife habitats within the southwestern United States, especially the impacts of increased demand for water resources within arid regions. A series of long-term studies on the Colorado River have shown that dam-induced habitat alternations have reduced overall bird abundance and diversity (Ohmart et al. 1977). Most of the once widespread riparian woodland along the Colorado River has been replaced by non-native salt cedar (*Tamarix* spp.) and shrubs typically found in intermittent drainages (Ohmart et al. 1977). Many of the birds requiring riparian woodland are no longer found along the Colorado River.

Many studies demonstrate how water impoundments impact birds and fish of riparian and aquatic habitats, but little is known about impacts on amphibians and reptiles inhabiting these ecosystems. Jones et al. (1985) and Jones and Glinski (1985) found that a number of mesic-adapted or upland amphibians and

reptiles were restricted entirely to cottonwood-willow riparian habitats within the Sonoran Desert. Usually found in habitats of the Upper Sonoran Life-zone (e.g., Chaparral), these species immigrated into lower elevations (< 762 m) of the Sonoran Desert via riparian corridors (Jones et al. 1985). Upland species occur on a few riparian sites within the Sonoran Desert that have maintained mesic habitat conditions (Jones et al. 1985). These conditions persist on these sites due to the moderating effects of leaf litter and logs resulting from cottonwood trees (*Populus fremonti*), perennial waterflow, shading of the surface by trees, and accumulation of large debris piles resulting from periodic flooding (Jones and Glinski 1985). In California, for example, riparian ecosystems provide habitat for 83 percent of the amphibians and 40 percent of the reptiles known from that state (Brode and Bury 1984).

Water impoundment structures eliminate periodic flooding and significantly reduce stands of cottonwoods and willows (*Salix goodingii*) along major drainages (Ohmart et al. 1977). These structures may, therefore, significantly reduce mesic conditions in downstream riparian ecosystems. To determine the possible impact of impoundment structures on the herpetofauna of a desert riparian ecosystem, I studied two low elevation (< 762 m) sites, one with major water impoundments and one without any impoundments.

Abstract.—Reptile abundance and diversity were greater on an unaltered riparian ecosystem than on an altered site; the former had some species typically found on upland habitats (e.g., chaparral) and the latter was comprised of species from adjacent Sonoran Desert. The distribution and abundance of certain microhabitats appear to account for differences in reptile abundance and diversity on the two sites.

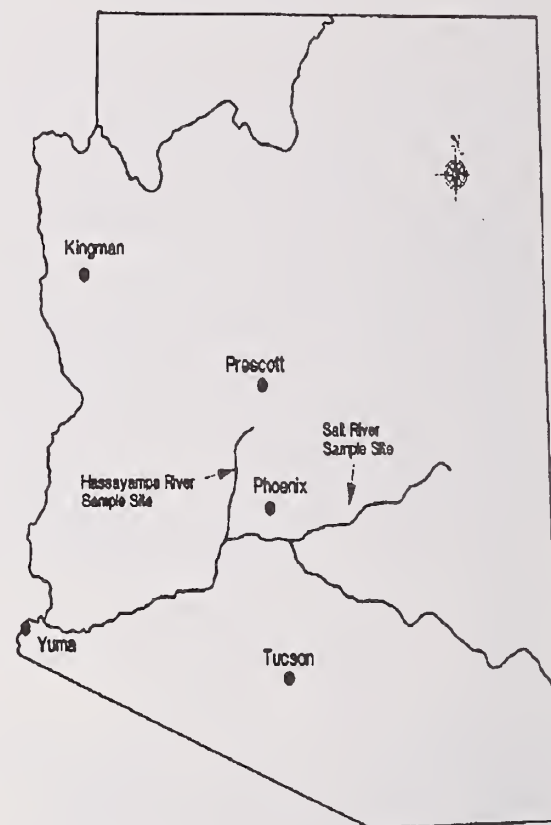


Figure 1.—Locations of the study areas.

Methods

To compare herpetofaunas of an unaltered vs altered desert riparian ecosystem, I chose study sites on the Hassayampa and Salt Rivers. The Hassayampa River has no major water impoundments. It originates in the Bradshaw Mountains 160 km north-northwest of Phoenix, Arizona, eventually draining into the Gila River approximately 80 km southwest of Phoenix. Lower reaches are mostly intermittent, except for a 15 km perennial section near Wick-

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enburg, Arizona. The study site was located approximately 10 km south of Wickenburg near Palm Lake, a former resort now owned by The Nature Conservancy, in a mature gallery-type stand of cottonwood (*Populus fremonti*) and willow (*Salix goodingii*) (elevation ca. 585 m, fig. 1).

The Salt River originates in east-central Arizona, flowing southwest to Granite Reef Dam (approximately 40 km northeast of Phoenix) where water is diverted for irrigation. Below this point, the floodplain traverses Phoenix, eventually draining into the Gila River approximately 26 km southwest of Phoenix. Historically, this river flowed perennially over its entire course. However, several major water impoundments, including dams forming Roosevelt, Apache, Canyon, and Saguaro lakes, have significantly altered flows and consequently physical characteristics. Flows are regulated by water releases at dams and flooding has nearly been eliminated; significant flooding has occurred only when water releases from lakes have been necessary. Before water impoundment, riparian vegetation was mostly cottonwood and willow, with mesquite (*Prosopis glauca*) occur-

ring primarily on vegas adjacent to the river (Reference?). Mesquite and tamarisk now dominate the riparian community, with only a few small (< 100 m in length) sections of cottonwood and willow. The Salt River sample site was at Blue Point, located approximately 6 km south of Saguaro Lake (fig. 1). Cottonwood, willow, and mesquite trees were common at this site, although cottonwoods and willows were not nearly as common as on the Hassayampa River. Blue Point's tree gallery was poorly developed and I found no evidence of tree reproduction. Substrate was dominated by sand, with gravel bars located intermittently throughout the site. Similar to the Hassayampa River site, several small drainages traversed this site.

The herpetofauna on each site was sampled by using a pit-fall trapping grid consisting of 110, double-deep 1.4 kg coffee cans placed 15 m apart in a 22 x 5 grid trapping configuration (1.9 ha) (see Jones 1987). Covers were placed approximately 15 cm above each trap to reduce loss of animals due to desiccation and exposure. Traps were open continuously between March and October, 1984. Traps were checked every three days, and amphibians and reptiles captured in traps were measured (snout-vent length, SVL), weighed, sexed, uniquely marked, and released into cover nearest to the capture site.

While traveling between pit-fall traps, I recorded observations of all frogs, toads, lizards, and snakes. I also flipped rocks and logs to uncover hidden herpetofauna.

In order to determine amphibian and reptile composition in adjacent Sonoran Desert, a modified array pit-fall trapping method was used (Jones 1987). Five arrays were placed in Sonoran Desert habitat adjacent to each site, and I checked these arrays for animals whenever I checked the main grids.

A point-center quarter (plotless) sampling method (Muller-Dumbois

and Ellenberg 1974) provided data to characterize microhabitats around each trap. Each trap was a center point for quantifying density and frequency of microhabitats within 7 m of each trap. I sampled 110 points or 440 quarters on each site. Microhabitat frequency was determined by dividing the number of quarters that a microhabitat occurred in (7 m or less from the trap) by the total number of quarters (440). I also estimated size (width, height, and depth) of each microhabitat and frequency of canopy cover as the percentage of pit-fall traps that were covered by vegetation (table 1).

Relative abundance equaled the number of an individual species trapped during a 24-hour period. I estimated the diversity of herpetofaunas and microhabitats on each site using a modified Shannon-Weaver diversity index (H') (Hair 1980): $H' = \sum p_i (\log_{10} p_i)$, where s = number of species and p_i = the proportion of the total number of individuals consisting of the i_{th} species. I used a Student's t -test to determine differences between herpetofaunas and microhabitats on the two sites. Finally, I compared herpetofaunas of the two riparian sites and adjacent Sonoran Desert by calculating Jaccard Similarity Coefficients and then clustered them using an unweighted pair group average (Pimental 1979).

Results

Microhabitats

The Hassayampa River had greater amounts and diversity of microhabitats than the Salt River (table 2). Of these differences, the frequency of downed litter on the two sites was the greatest (table 2). Leaf litter was 3 times more common, debris heaps 10 times more common, and logs and limbs twice as common on the Hassayampa River than on the Salt River (table 2). Rock substrate and grasses were more common on the Has-

Table 1.—List of microhabitats measured at or around each pit-fall trap on each river. Frequency equals the percentage of quarters around each trap that had a certain microhabitat.

Soil type (at trap)	Rock width
Vertical cover (over trap)	Rock frequency
Distance to leaf litter	Distance to tree
Leaf litter depth	Tree height
Leaf litter frequency	Tree width (crown)
Distance to log	Tree frequency by species
Log diameter	Distance to shrub
Log frequency	Shrub height
Distance to debris heap	Shrub width (crown)
Debris heap width	Shrub frequency
Debris heap depth	Distance to grass Patch
Debris heap frequency	Grass height
Distance to rock	Grass frequency

sayampa River and shrubs on the Salt River (table 2). Trees were common on the Hassayampa River and sand substrate on the Salt River, although neither of these differences were significant (table 2). In addition, average leaf litter depth was significantly greater on the Hassayampa River than on the Salt River (table 2).

Of the specific types of canopy covering pit-fall traps, trees were by far the most common on both rivers, although the Salt River had more pit-fall traps with no canopy cover (fig. 2).

Tree composition varied considerably between sites. The Hassayampa River had more cottonwoods (*Populus fremonti*) and willows (*Salix goodingi*) and the Salt River more salt cedars (*Tamarix* spp.) (fig. 3). Mesquite (*Prosopis glandulosa*) was the most common tree on both sites (fig. 3).

The Hassayampa River had more trees in the 0-1.9, 5.0-9.9, and 10.0-14.9 m height ranges, but most at the Salt River were in the 2.0-4.9 m range (fig. 4). Cottonwood height distribution was relatively even on the Hassayampa River, but most Salt River cottonwoods were greater than 10 m, with none less than 5 m, hence no reproduction (fig. 5).

Herpetofaunas

The abundance and diversity of herpetofauna was greater on the Hassayampa River than on the Salt River. The Hassayampa River had nearly twice as many species, more than twice the number of individuals, and a greater species diversity (1.05 vs. 0.86) than the Salt River (fig. 6).

All but three species (*Bufo microscaphus* x *woodhousei*, *B. punctatus*, and *Cnemidophorus tigris*) were more abundant on the Hassayampa River, and this site had five "upland" species (*Cophosaurus texanum*, *Diadophis punctatus*, *Eumeces gilberti*, *Masticophis bilineatus*, and *Tantilla*

hobartsmithii) usually found in habitats of the Upper Sonoran Life-zone (e.g., chaparral). These upland species were absent from the Salt River and adjacent Sonoran Desert (table 3). *C. tigris* had the same abundance on both rivers, *C. tigris* was the most abundant species on the Salt River, and *E. gilberti* was the most abundant

species on the Hassayampa River (table 3). The Hassayampa River also had 4 species with abundances greater than 1.0, whereas the Salt River only had one (table 3).

A cluster analysis of Jaccard Similarity Coefficients using data in table 3 revealed that the Salt River riparian site had a herpetofauna more similar

Table 2.—Comparison of microhabitat abundance between the Salt and Hassayampa Rivers. Abundance is the mean number quarters in which a microhabitat was found around each trap (within 7 m) \pm SD.

Microhabitat	Salt River	Hassayampa River	Significant Difference (p < .05)
Rocks	0.5 \pm 0.4 (55)	1.9 \pm 0.7 (209)	Yes
Sand substrate	3.8 \pm 0.2 (418)	3.0 \pm 0.5 (326)	Yes
Leaf litter	0.9 \pm 0.5 (99)	3.7 \pm 0.8 (407)	Yes
Logs/downed tree limbs	1.5 \pm 0.7 (165)	3.8 \pm 0.2 (422)	Yes
Debris heaps	0.2 \pm 0.2 (18)	1.1 \pm 0.3 (123)	Yes
Trees	1.9 \pm 0.7 (213)	2.9 \pm 0.6 (315)	No
Shrubs	2.7 \pm 1.3 (297)	2.5 \pm 1.1 (275)	No
Grass	0.4 \pm 0.3 (48)	1.2 \pm 0.4 (128)	Yes
Microhabitat diversity (H')	.77	.87	

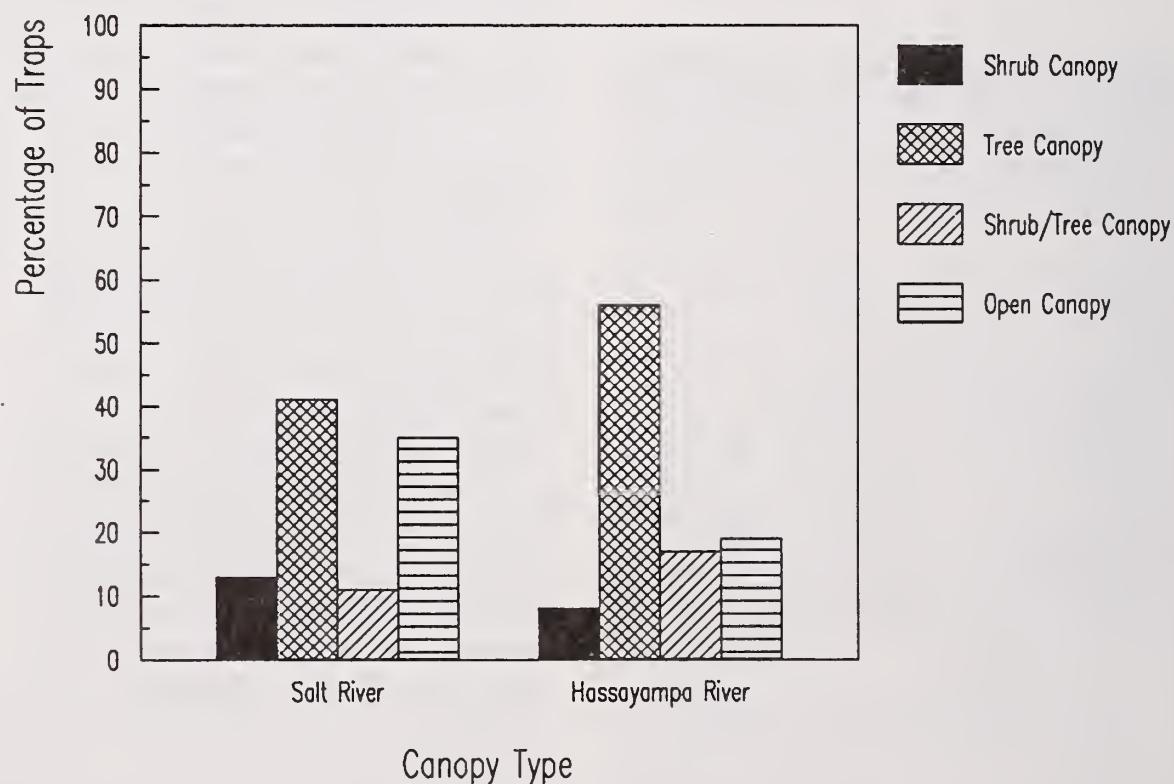


Figure 2.—Comparison of canopy types on the Salt and Hassayampa Rivers.

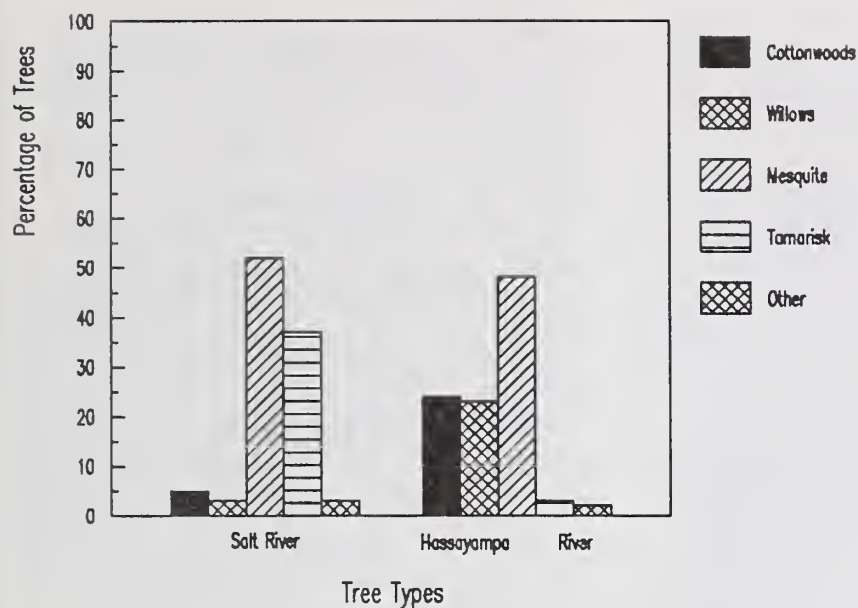


Figure 3.—Comparison of tree composition on the Salt and Hassayampa Rivers.

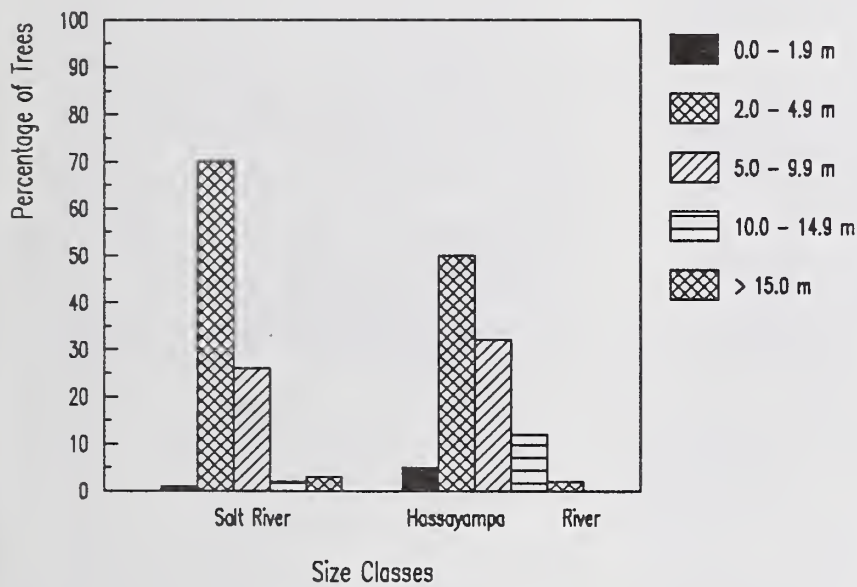


Figure 4.—Comparison of tree height distribution on the Salt and Hassayampa Rivers.

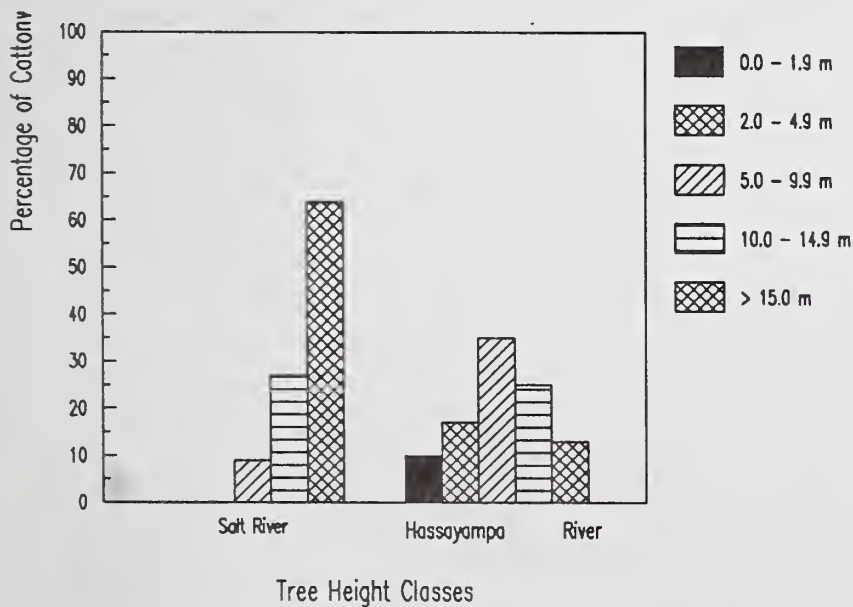


Figure 5.—Comparison of size classes of cottonwoods on the Salt and Hassayampa Rivers.

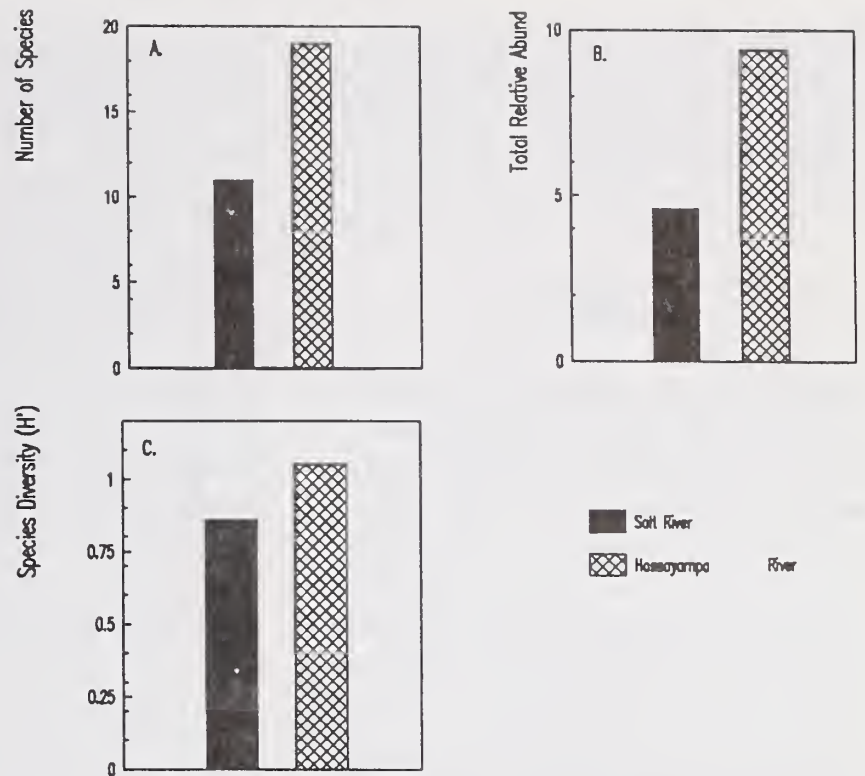


Figure 6.—Comparison of the total number of amphibians and reptiles, total relative abundance, and species diversity on the Salt and Hassayampa Rivers.

Table 3.—Comparison of lizard abundance and diversity between the Salt vs. Hassayampa River. Abundance is the number of lizards caught/grid/24 hours. Amphibians and reptiles occupying adjacent Sonoran Desert habitats also are indicated.

Species	Salt River	Hassayampa River	Sonoran Desert
<i>Callisaurus draconoides</i>	0.27	0.60*	X
<i>Cnemidophorus tigris</i>	1.47	1.47	X
<i>Coleonyx variegatus</i>	0.03	0.03	X
<i>Leptotyphlops humilis</i>	0.07	0.23*	—
<i>Sceloporus magister</i>	0.47	1.27*	X
<i>Thamnophis cyrtopsis</i>	0.07	0.10	—
<i>Urosaurus ornatus</i>	0.67	1.10*	X
<i>Uta stansburiana</i>	0.07	0.17*	X
<i>Bufo microscaphus</i> x <i>woodhousei</i>	0.40*	0.23	—
<i>Bufo punctatus</i>	0.57	0.40	X
<i>Scaphiopus couchi</i>	0.50	0.63	X
<i>Cophosaurus texanus</i>	—	0.20*	—
<i>Diadophis punctatus</i>	—	0.10*	—
<i>Eumeces gilberti</i>	—	2.17*	—
<i>Lampropeltis getulus</i>	XX	0.07*	X
<i>Masticophis lateralis</i>	—	0.07*	—
<i>Sonora semiannulata</i>	—	0.10*	X
<i>Tantilla hobartsmithi</i>	—	0.37*	—
<i>Bufo alvarius</i>	—	0.23*	—

*Significantly greater abundance at $p < .05$.

X Verified in adjacent Sonoran Desert habitats via pit-fall trapping.

XX Verified on the Salt River site via field search.

to adjacent Sonoran Desert than to the herpetofauna of the Hassayampa River riparian site, although the two riparian herpetofaunas were relatively similar (fig. 7).

Discussion

The distribution, abundance, and diversity of herpetofauna on the Salt River correlate with impoundment-induced changes in microhabitats. On the unaltered riparian ecosystem on the Hassayampa River, many microhabitats were more abundant and diverse than on the Salt River, especially surface litter and trees. These differences in microhabitats correlate with differences in species diversity and abundance on the two rivers. Species that were most abundant on the Hassayampa River (*Eumeces gilberti*, *Sceloporus magister*, and *Urosaurus ornatus*) prefer sites with downed vegetative litter and vertical structure (e.g., trees) (Jones and Glinski 1985, Jones 1986). These reptiles were not nearly as common on the Salt River and this may result from lower surface litter and vegetation structure (higher percentage of salt cedar, *Tamarix* spp., and a lower percentage of cottonwoods, *Populus fremonti*, and willows, *Salix goodingii*) on this site.

The greatest difference between herpetofaunas on the two rivers was presence of five upland species on the Hassayampa River and the absence of these species on the Salt River. Jones and Glinski (1985) suggested these species occur in riparian habitats within low elevation Sonoran Desert because of the moderating effects of certain microhabitats, especially surface litter and debris heaps. Surface litter and debris heaps are considerably less common on the Salt River, and this probably accounts for the lack of any upland species in this river's herpetofauna. Szaro et al. (1985) suggest that debris heaps are the principal source of food and cover for *Thamnophis elegans*, and

that grazing-caused reduction in this microhabitat caused decline of this snake in a high elevation riparian community.

The relatively low amounts of surface litter and lack of smaller size classes of trees (especially cottonwoods and willows) on the Salt River appear to result from dam-induced changes in water flow and flooding. Periodic flooding is essential in the long-term maintenance of southwestern U.S. riparian ecosystems (Brady et al. 1985). Flooding also provides the physical mechanism by which large debris piles are built (Jones and Glinski 1985). Water impoundment structures on the Salt River appear to prevent flooding regimes necessary to maintain cottonwood reproduction and debris piles.

Over the past 10 years, the major emphasis in riparian management has been to manage trees, particularly cottonwoods. Several techniques, such as planting live trees and tree poles, have been used on drainages with major water im-

poundment structures to improve reproduction and survival of cottonwoods (Swenson and Mullins 1985). Although these techniques generally increase nesting habitat for birds, they do not provide enough surface litter to support litter-dwelling species, such as upland herpetofauna. Szaro and Belfit (1986) studied a artificially created stand of riparian vegetation on Queen Creek in south-central Arizona. This stand of mostly willows resulted from accumulation of water behind a dike. Although the stand emulated vegetation structure of natural riparian sites, it had a depauperate herpetofauna, even after 20 years.

This study suggests surface litter is important in determining abundance and diversity of herpetofaunas in riparian communities. If we are to conserve riparian ecosystems, we must increase our emphasis on protecting all habitat components, including microhabitats such as surface litter. Like the Salt River site, riparian areas will lose litter-dwelling and

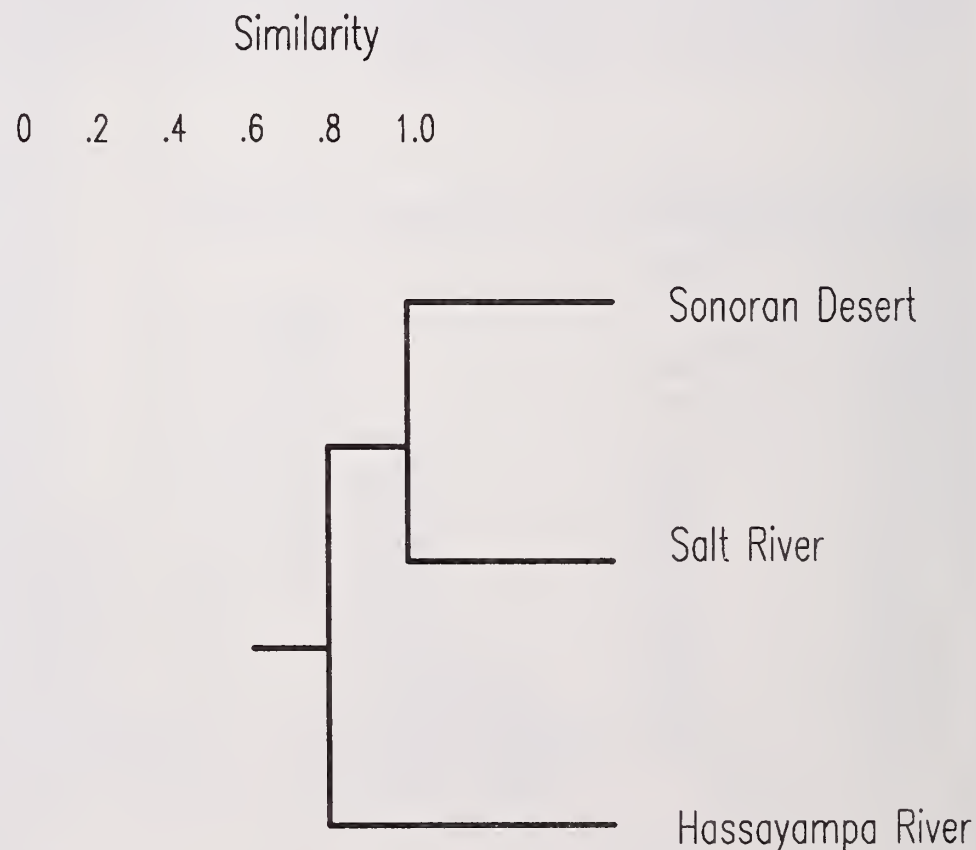


Figure 7.—Dendrogram comparing herpetofaunas of the Sonoran Desert and Salt and Hassayampa Rivers.

mesic-adapted species unless we consider these other components.

Acknowledgments

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Critical Habitat, Predator Pressures, and the Management of *Epicrates monensis* (Serpentes: Boidae) on the Puerto Rico Bank: A Multivariate Analysis¹

Peter J. Tolson²

Epicrates monensis is a small (ca. < 1 m snout-vent length) semi-arboreal boid snake (fig. 1) that exhibits an extremely disjunct distribution on the Puerto Rico Bank. The Mona boa (*E. m. monensis*) is endemic to Isla Mona, a large island in the Mona Passage between Hispaniola and Puerto Rico (Schmidt 1926). The other subspecies, the Virgin Islands boa (*E. m. granti*), is found on scattered islands and cays from La Cordillera eastward through the Virgin Islands, including St. Thomas, Tortola, and Virgin Gorda (Stull 1933; Nellis et al. 1984; Mayer and Lazell 1988). The boa is apparently absent from Puerto Rico and the other large islands on the bank. Judging from the present distributions, the historical range of *Epicrates monensis* encompassed virtually the whole length of the Puerto Rico Bank. Today, unfortunately, the snake is endangered (USFWS 1980) and absent from far more islands on the bank than it is resident—doubtless the result of a long history of extirpation. It is improbable that the decline of the boa can be traced to a single causative factor; more likely the survival of the snake at certain localities is due to a complex series of biotic, environmental, and stochastic

interactions. The rarity of the snake has made habitat analysis difficult; one cannot define critical habitat if the snake cannot be observed. Prior to my work, fewer than 13 specimens of the boa had been encountered, and habitat descriptions were largely anecdotal with no attempts to quantify those factors important in determining population levels (Div. of Fish and Wildlife, USVI 1983; USFWS 1984, 1986).

The parameters dictating the distribution and abundance of animal species within a habitat are often diverse. They include not only the physical structure of habitat, such as vegetational composition and spatial heterogeneity (Rotenberry and Wiens 1980), but also species composition (Matthews 1985; Moulton, 1985) and other aspects of community structure which are less easily defined, such as competition (Cody 1974) or predation pressure. In the West Indies, particularly on the Puerto Rico Bank, utilization of a particular habitat by the endemic herpetofauna is not only dependent on the structural attributes of vegetative cover and the composition of the endemic animal communities, but also on the number and severity of feral and exotic animal introductions that have occurred. Colonizations (accidental or otherwise) of the roof rat, *Rattus rattus*, the house cat, *Felis catus*, and the mongoose, *Herpestes auropunctatus*, have profoundly influenced the survival and distribution of endemics on

Abstract.—*Epicrates monensis* is an endangered boa endemic to the Puerto Rico Bank. Principal components analysis, based on data collected during five years of study and 200 captures of this species, was used to identify predator, prey, and habitat variables critical to survival of the snake. Management recommendations are discussed.

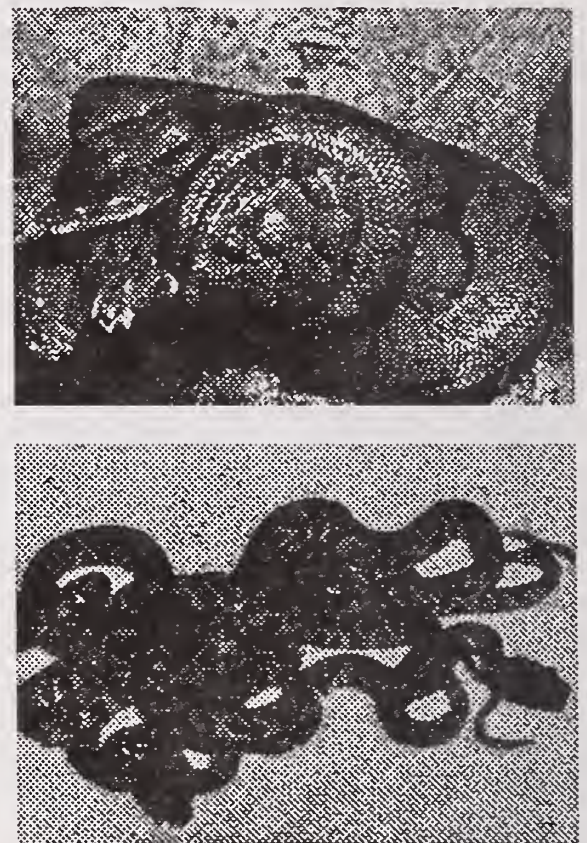


Figure 1.—*Epicrates monensis granti*. Above—adult female, Cayo Diablo, Puerto Rico. Below—juveniles born at the Toledo Zoological Gardens 14 July 87.

the Puerto Rico Bank (Barbour 1917, 1930; USFWS 1986; Div. of Fish and Wildlife, USVI 1983).

Principal components analysis (PCA) is a multivariate statistical technique that has been used by community ecologists to model distributions of animal populations in a multidimensional habitat space defined by a correlation matrix of habitat variables (See Wiens and Rotenberry 1981 and Matthews 1985). My current work with *Epicrates monensis* utilizes PCA to correlate the abun-

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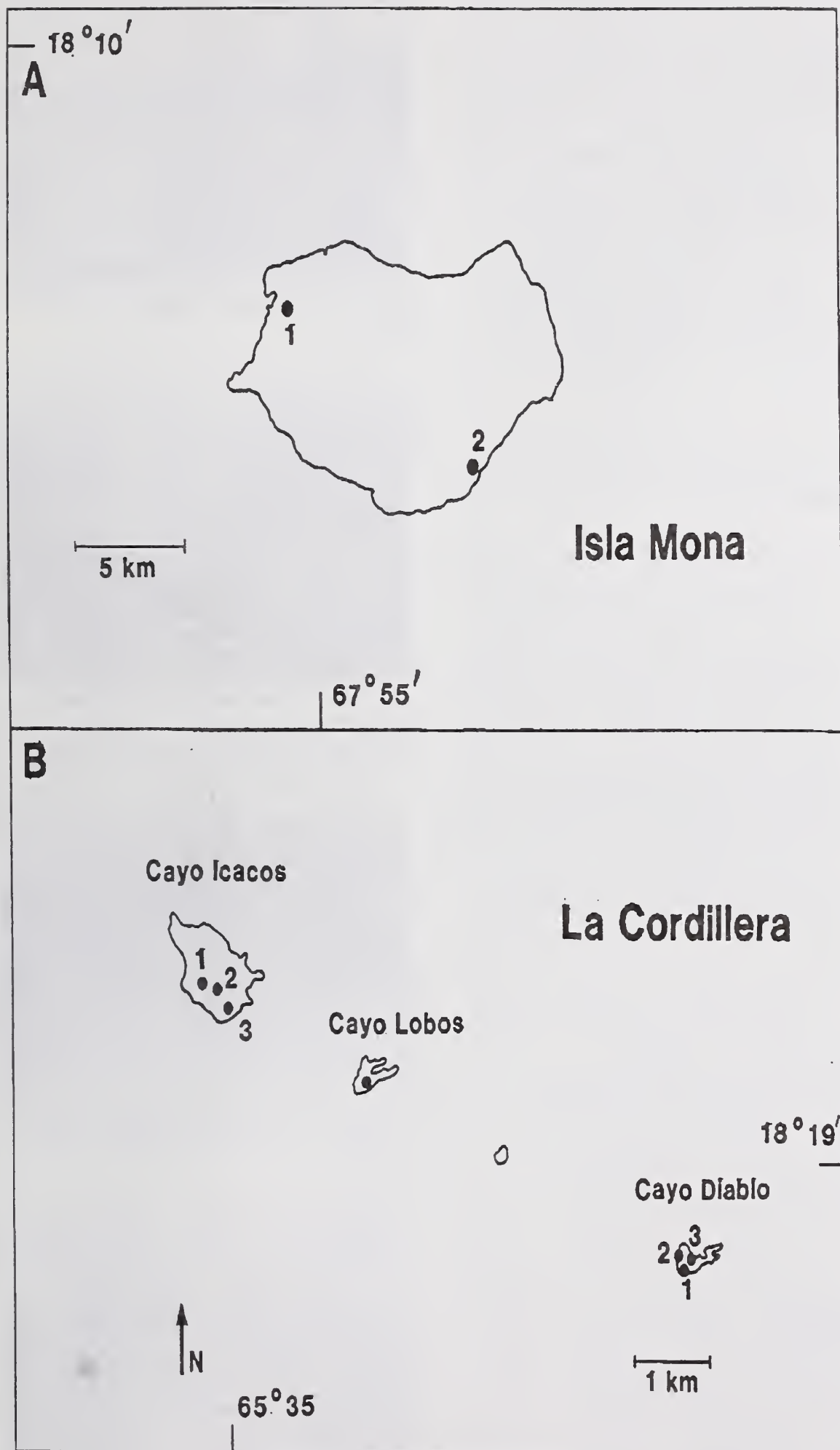


Figure 2.—Location of sampling plots in Puerto Rico. Above—plots on Isla Mona. Below—plots on La Cordillera.

dance of the boa with certain critical elements of habitat structure and indices of population densities of preferred prey species and predators. Compilation of such data is extremely important in establishing the critical dimensions of the boa niche, the identification of suitable release sites for snakes born in captivity, and the selection of likely search localities for surveys of previously undescribed populations of the snake. By using PCA, we also hoped to extract independent patterns of covariation, such as the degree of niche overlap with *Alsophis*, which might explain certain distributional anomalies of the boa populations.

Methods

Study Areas

This study is based on habitat analysis of 24 different localities on the following islands and cays of the Puerto Rico Bank: Buck Is., Cas Cay, Cayo Diablo, Cayo Icacos, Cayo Lobos, Congo Cay, Great St. James Cay, Isla Mona, Outer Brass Cay, Salt Cay, Saba Cay, and Steven Cay from February 1986 through April 1988. Some islands had several plots. Sites were chosen at random without regards to presence or absence of boas, but an attempt was made to select sites so that sampling included the full spectrum of habitat available to the boa. Figures 2 and 3 illustrate the location of sampling plots included in the study.

Vegetational Profiles of Study Sites

Subtropical dry forest is the habitat where *E. monensis* is most commonly observed, particularly on Isla Mona and St. Thomas. It is characterized by small (< 5 m) deciduous trees with small, coriaceous or succulent leaves and thorns, spines, and secondary defensive compounds (Ewel and Whitmore 1973). Examination of the

present range of the boa indicates that it matches the occurrence of dry subtropical forest on the Puerto Rico Bank (Ewel and Whitmore 1973). This is most apparent on St. Thomas, where *E. monensis* is restricted to the dry eastern end of the island despite presumably suitable habitat elsewhere (Nellis et al. 1984). Common tree species include *Burseria simaruba*, *Cephalocereus royenii*, *Pictetia aculeata*, *Bucida buceras*, *Guaiacum officinale*, *Leucaena glauca*, *Tamarindis indica*, *Melicoccus bijugatus*, *Acacia* ssp., and *Capparis cynophallophora* (Little and Wadsworth 1964). In addition, on our dry forest plots (Cas, Icosos 1, Congo 1, Outer Brass 1, and Gt. St. James 1), we encountered many *Byrsonima lucida*, *Euphorbia petiolaris*, and *Metopium toxiferum*. On Buck 1, Diablo 1, Gt. St. James 3, and Mona 2 the vegetation consisted of tree species with compound trunks, primarily *Coccoloba uvifera*, *Hippomane mancinella*, and *Thespesia populnea*. Sabal palm groves were present on Outer Brass 2 and Salt 2. Salt-tolerant shrublands primarily composed of *Suriana* and *Tournefortia* just above the high tide line was the dominant vegetation on Diablo 2, while Diablo 3 primarily

consisted of *Cassythia/Opuntia* tangles. *Ficus*-dominated forest was present on Mona 1 and Congo 2. Guinea grass, *Panicum maximum*, dominated the transect on Buck 2 and *Acacia macracantha* on Buck 3. A basic summary of the vegetation of the smaller cays is given in Heatwole et al. (1981). Figures 4 through 7 illustrate four typical vegetational types at transect sites: *Coccoloba* grove (Buck 1), mixed palm/shrubland (Diablo 2) *Opuntia/Cassythia* tangles (Diablo 3) and grassland (Buck 2).

Geomorphology and Topography of Study Sites

Geomorphology of the various islands and cays studied varied considerably, from the steep-sided metamorphic topography of St. Thomas and associated cays (Heatwole et al. 1981) to the cemented dune structure of La Cordillera (Kaye 1959a). Isla Mona is composed primarily of a Pleistocene limestone plateau surrounded by sheer cliff (Kaye 1959b). In fact, most islands of the bank have significant limestone deposits, with varying amounts of metamorphic rock, in-

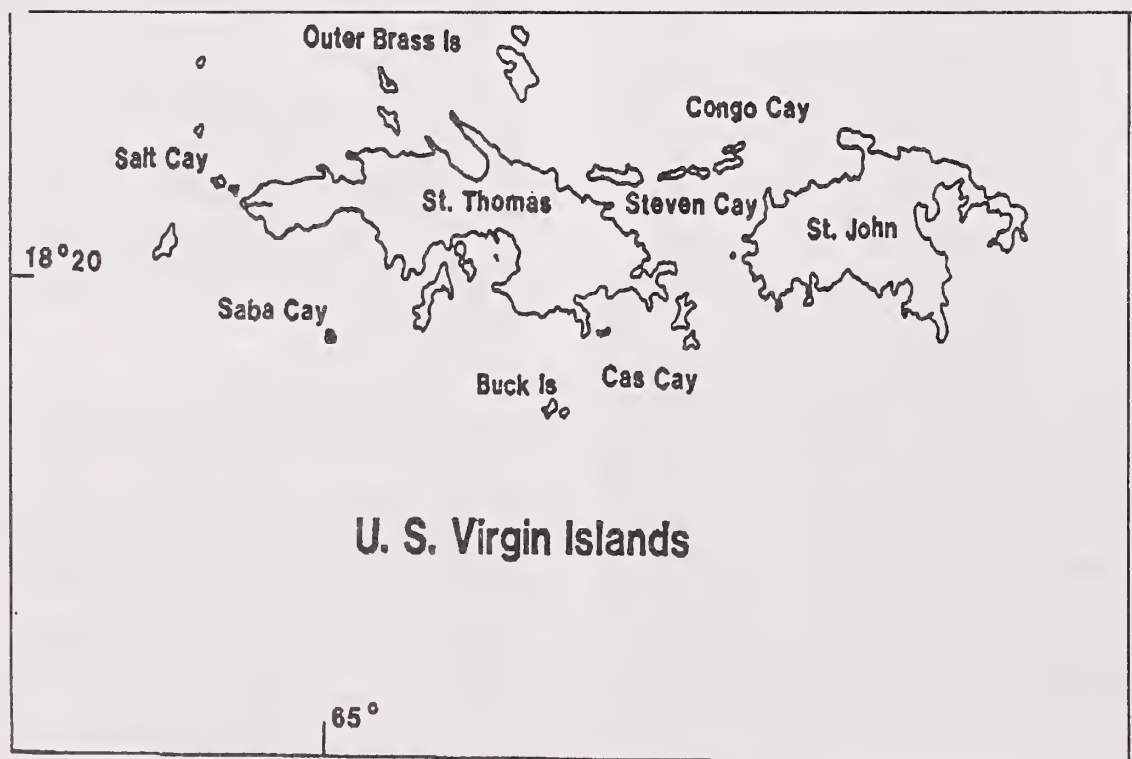


Figure 3.—Location of sampling plots, U.S. Virgin Islands.



Figure 4.—*Coccoloba uvifera* habitat on Buck 1.

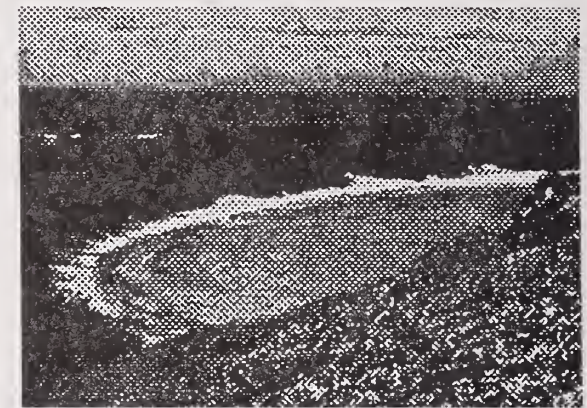


Figure 5.—Mixed *Cocos* and scrubland habitat on Cayo Diablo. The vegetation at the center of the island is primarily *Cassythia* vine growing over *Opuntia* cactus.

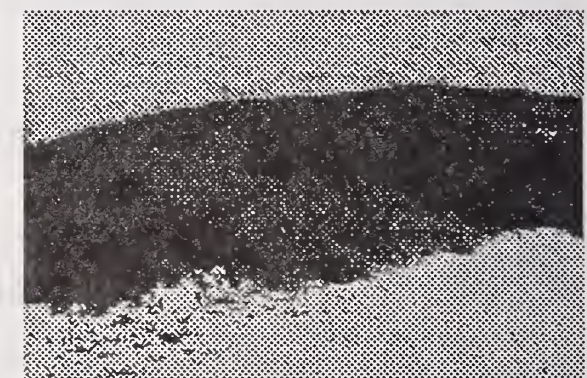


Figure 6.—Aromatic beachfront shrubland, primarily *Suriana* and *Tournefortia*, near Diablo 2.

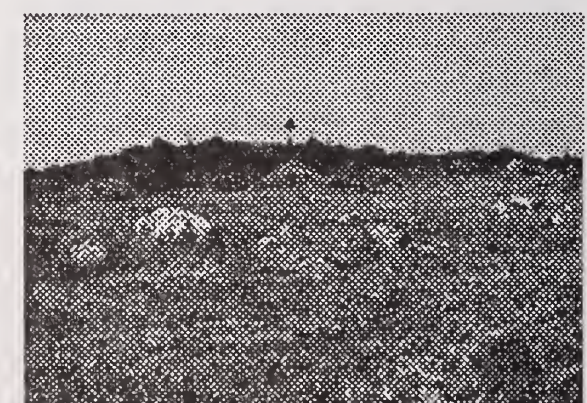


Figure 7.—Guinea grass, *Panicum maximum*, habitat on Buck 2.

cluding gneiss and basalt, present as well. The cays of La Cordillera are exceedingly low, with maximum elevations under 15 m. In the Virgin Islands the cays are of moderate elevation with eroded limestone hills approaching 50-300 m in height. An overview of the geology of the Virgin Islands is given in Schuchert (1935).

Climate

The climate of the Bank is essentially subtropical to tropical. Temperatures of the coastal areas range from overnight lows of ca. 15° C to daytime highs approaching 35° C. Rainfall, especially on Puerto Rico, is geographically variable (Briscoe 1966). Areas within the range of *E. monensis* typically receive < 750 mm of rainfall per year.

Sampling Techniques

The presence or probable absence of the boa on a particular cay was determined by active searching of all habitat types during surveys (carried out independently of habitat analysis) from April 1983 to September 1987. Typically 2 weeks or more were

spent searching larger islands and three to five days for smaller cays. Only 1 night was spent on Cayo Lobos, as the native vegetation was all but completely destroyed by human activity and all densely vegetated areas could be searched repeatedly in a single night. Our experience with multiple recaptures of the same individual indicates that the snakes forage every night under most circumstances. Within each 24-hour period 4 hours per night were spent searching likely foraging sites such as vine tangles, terminal branches of trees, palm crowns, and beachfront vegetation. During the daylight hours, refugia sites such as debris piles, termite nests, and palm axils were examined. After capture, the time, capture height, habitat description, ambient temperature, refugium temperature, and cloacal temperature of each snake were recorded. Later, sex, body mass, snout-vent length (SVL), and caudal length (CL) were recorded. The snakes were examined for reproductive condition, presence of injuries, and parasite infestation. Snakes were marked using the technique of Brown and Parker (1976) and released at the point of capture.

Habitat variables recorded included both physical and biological

parameters (table 1). Predator density estimates include indices of abundance for likely predators of *E. monensis*: the roof rat, *Rattus rattus*, the pearly-eyed thrasher, *Margarops fuscatus*, and the Puerto Rican racer, *Alsophis portoricensis*. *Rattus* densities were estimated using removal trapping over a 3-day span on 100-m transects with Victor snap traps spaced every 5 m. Presence of *Felis catus* was determined by direct observation. Because of the extreme wariness and trap-shy nature of the *Felis* on study plots, only their presence or absence was recorded.

Prey density data includes of population densities for *Anolis cristatellus* and *Ameiva exsul*. *Anolis*, *Alsophis*, *Ameiva*, and *Margarops* were counted by having two observers slowly walk the transects and counting the individuals of each species observed within a 5 m distance on each side of the transect line. On Cayo Diablo, independent estimates of *Ameiva* and *Anolis cristatellus* populations were gathered by surveys of 5 m² quadrats. *Anolis cristatellus* perch heights were measured with a metric tape except on Cayo Lobos and Salt Cay. Canopy height was estimated for each habitat with the help of a metric tape. Vegetative composition was determined by subjective stratified sampling using 10 m² quadrat plots (Clarke 1986); plant samples were taken for species identification from each island. Vegetation coverage data indicates the percentage composition of five different classes of vegetation: trees (trunk circumference at shoulder height > 25 cm), palms, *Opuntia* cactus, shrubs and small trees (trunk circumferences < 25 cm), and grasses. Vegetation structural data includes the number of dominant plant species, the height of the canopy, and the continuity of the vegetation (a measure of the difficulty for the boa to crawl from one plant to another without going to the ground). Plants were identified by David W. Nellis and the author.

Table 1.—Factor patterns of the original variables on each of the first six principal components.

Variable	Principal component					
	I	II	III	IV	V	VI
Rat density	-0.6795	-0.3582	0.0162	-0.2453	0.4298	-0.0379
Cat presence	0.4976	0.1703	0.0895	-0.4592	-0.3190	-0.2217
Racer density	-0.4702	0.0838	-0.1051	0.5491	-0.1627	-0.0437
Thrasher density	-0.5268	0.2052	0.0410	0.0091	-0.6211	0.4070
<i>Anolis</i> density	-0.1400	0.3391	0.4005	0.4582	0.1560	-0.4850
<i>Ameiva</i> density	-0.0657	0.6091	-0.5302	0.3176	-0.0890	-0.0628
<i>Anolis</i> perch height	0.7972	0.1830	-0.1991	-0.0386	0.2946	-0.0233
Compound tree density	-0.0810	0.7175	-0.4546	-0.2118	0.2106	0.0407
Single tree density	-0.5156	-0.0546	0.3885	0.1877	0.5079	0.2290
Palm density	0.4478	0.1154	0.3690	-0.5638	-0.2063	0.0771
Shrub density	0.6215	-0.3240	0.4724	0.4028	-0.1720	-0.0718
Grass density	-0.1656	-0.5586	-0.5118	-0.1659	-0.0554	-0.4613
Cactus density	0.3458	-0.3437	-0.1861	0.3130	0.1391	0.6288
Vegetational continuity	0.6882	0.3989	-0.0270	-0.1124	0.3701	0.0988
Canopy height	-0.3978	0.7730	0.4023	-0.1372	0.0139	0.0257

I attempted to use continuously distributed standardized environmental variables whenever possible. Absence of a particular predator or prey species on a given a sample plot did not always indicate its absence from the island on which the plot was situated. Only male *Anolis* perch heights were used for the statistical analysis, as female and juvenile *A. cristatellus* tend to frequent the ground under all circumstances (Kiest et al. 1975). Mean male *Anolis* perch height data were pooled for each island for character 16 of the PCA data matrix, as some plots were completely devoid of *Anolis*.

Statistical Analysis

Principal components analysis was performed using the Statistical Analysis System "SAS" release 5.16 (SAS Institute 1985). Significant habitat components, which included both biotic and structural variables of the collecting localities (e.g. those which accounted for > 10% of the total variance in the data), were clustered on the basis of their association within the PCA data matrix. The second step of the analysis compared the relative abundance of *E. monensis* at each collecting locality with habitats described by the significant axes of the principal components. Regression analysis, ANOVA, and descriptive statistics (mean, standard deviation, etc.) were performed using Statview 512³ on an Apple Macintosh Plus.

Results

Multivariate Analysis of Habitats

The PCA indicates that biotic factors, plant composition, and structural at-

tributes of vegetation are all important contributors to variance in the PCA patterns. Factor patterns for the first six principal components are given in table 1. Principal component I accounts for 23.4% of the variance. This component clusters habitats with high shrub and palm densities, low numbers of single trees, vegetational continuity, and low canopy heights. Important biotic characteristics of this space include *Felis* presence and low *Rattus*, *Margarops*, and *Alsophis* densities with high *Anolis* perch heights. Principal component II accounts for an additional 17.0% of the variance observed. This axis describes sites having low grass density, high compound tree densities, canopy height > 3 m, and high *Ameiva* densities. Principal component III accounted for 11.2% of the variance and suggested an association between low *Ameiva* density, low compound tree density, low grass density, high shrub density, and canopy height > 3 m. Factor IV accounted for another 10.7% of the variance and clustered high *Alsophis* and *Anolis* densities with *Felis* absence and low palm density. Components V-VI were less significant in the PCA (e.g. each accounted for < 10 % of the variance) but added some interesting ecological information to the habitat analysis. Principal component V clustered high *Rattus* density with low *Margarops* density; principal component VI grouped high *Margarops* density with low *Anolis* density.

Habitat Utilization by *Epicrates monensis*

The vegetational profiles of climax plant communities (and *E. monensis* collection localities) in the dry forest may differ considerably depending on island size, geology, geomorphology, rainfall, and history of human or feral mammal disturbance. However, most dry forest habitats on the Bank are structurally simple, with usually

only two to five dominant plant species (table 2). Captures and sightings of the Mona boa have been limited to three distinct localities: dry plateau forest adjacent to Uvero and Pajaros (Campbell and Thompson 1978; Rivero et al. 1982) *Coccoloba uvifera* groves of Pajaros (M. Frontera, Pers. Comm.), and Cocos groves and nearby vegetation adjacent to Playa Sardinera (G. Rodriguez pers. comm.). The Virgin Islands boa has been encountered repeatedly on only two islands: St. Thomas and Cayo Diablo. All specimens from St. Thomas were captured on the east end of the island near Red Hook. Two specimens were found beneath a limestone slab during construction of the Vessup Bay Estates housing subdivision, another was taken from a stone wall, and a third was found as a roadkill near Smith Bay. R. Thomas captured a specimen crawling in a viney tangle ca. 2.4 m high (Sheplan and Schwartz 1974).

The Red Hook area is dominated by xeric forest composed primarily of *Burseria*, *Croton*, and *Acacia*. No habitat data is available for *E. m. granti* on Tortola. I have received reports that the boa was present in the palm forest of Outer Brass Island (J. LaPlace pers. comm.) but I was unable to find it there even after five trips to the island. Virgin Islands residents also report the boa as inhabiting Great St. James Is. (D. Nellis pers. comm.), Great Camanoe, Necker Is., and Virgin Gorda, (Mayer and Lazell 1988), but these sightings have not been confirmed by biologists. Grant (1932) mentioned anecdotally (he did not capture the holotype himself) that "the boa is found on rocky cliffs on Tortola and Guana Islands."

On Cayo Diablo, *Coccoloba uvifera* is the habitat most commonly associated with foraging *E. monensis*. Of the 79 active snakes we captured, 51 were found in *Coccoloba*, ten in *Caesalpineia*, nine on *Cassythia*, seven in *Suriana*, and two in *Opuntia*. Twenty-three percent of the snakes were ac-

³The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U. S. Department of Agriculture to the exclusion of others that may be suitable.

tive at heights > 2 m. Of these, 67% had SVLs > 400 mm. Seventy-five percent of juvenile snakes (under 300 mm SVL) foraged at heights < 1.5 m, but regression analysis indicated that these differences were not statistically significant. Of the 149 inactive snakes taken from refugia, 43% were in *Cocos* or *Sabal* axils, 36% were in termite nests, and 21% were under rocks or debris. Fifty-one percent of snakes taken from termite nests were females; over half of these were gravid. Gravid females use termite nests or sun-baked debris to thermoregulate and may elevate their body temperatures to over 33°C.

Prey Density and *Epicrates monensis* Distributions

The greatest concentrations of *Epicrates monensis* are in areas (particularly *Coccoloba* groves) with *Anolis* densities > 60 *Anolis*/100 m².

This *Anolis/Epicrates* association is reinforced by PCA (see below). My field logs indicate that the greatest success in finding foraging *Epicrates* occurs when observations of sleeping *Anolis* are > 12 lizards/h. Numerical counts of sleeping *Anolis* and the times between sightings are regularly noted in my field book as a rough guide to potential hunting success in a study locality.

Anolis cristatellus is the primary prey species of *E. monensis*, and the mean foraging height of the snake (\bar{x} = 1.356, SD = 1.079 N = 54) is close to the mean perch height of sleeping *Anolis* (\bar{x} males = 1.816 m, SD = 0.993, N = 17; \bar{x} females = 1.323 m, SD = .681, N = 14; \bar{x} juveniles = 1.417 m, SD = 0.169, N = 5).

High *Ameiva* densities are also a common component of localities with high boa densities, although I observed only one instance of a boa feeding on *Ameiva*, which are strongly diurnal.

Feral Mammal Abundance and *Epicrates monensis* Distributions

Of the 10 islands surveyed for this study, only three were completely devoid of rats: Cayo Diablo, Cayo Icacos, and Steven Cay. These islands have high *Ameiva* and *Anolis* densities, but only Diablo Cay harbors a population of the boa. It also has the highest densities of *Epicrates monensis* found anywhere on the bank, > 100 snakes/hc at some localities. Those islands with heavy rat densities (ca. 20 rats/hectare)—Buck Is., Cas Cay, and Salt Cay—have lower *Ameiva* and *Anolis* densities and apparently no boa populations, despite suitable habitat. Rat densities are not always correlated with low *Anolis* densities, however. Some islands, such as Outer Brass and Congo, have *Anolis* densities apparently high enough to support populations of the boa, but their perch heights (table 2) are significantly different from those *Anolis*

Table 2.—PCA habitat matrix for the Puerto Rico Bank.

	Rat dens.	Cat presence	Racer dens.	Thrasher abund.	<i>Anolis</i> dens.	<i>Ameiva</i> dens.	Comp. tree dens.	Single tree dens.	Palm dens.	Shrub/ small tree dens.	Grass dens.	<i>Opuntia</i> dens.	Contig. veg. cover	Plant diver.	Canopy height	<i>Anolis</i> perch height
Cayo Diablo 1	0.00	0	0.00	0.00	1.48	1.50	0.99	0.00	0.01	0.00	0.00	0.00	1.00	1	1.00	1.70
Cayo Diablo 2	0.00	0	0.00	0.00	0.25	0.05	0.00	0.00	0.03	0.95	0.00	0.00	1.00	2	0.50	1.70
Cayo Diablo 3	0.00	0	0.00	0.00	0.00	0.10	0.00	0.00	0.00	1.00	0.00	0.50	1.00	3	0.25	1.70
Cayo Icacos 1	0.00	1	0.00	0.05	0.36	0.75	0.46	0.05	0.00	0.50	0.00	0.00	0.75	4	1.00	1.57
Cayo Icacos 2	0.00	1	0.00	0.00	0.91	0.00	0.14	0.10	0.13	0.63	0.00	0.00	0.50	6	1.00	1.57
Cayo Icacos 3	0.00	1	0.00	0.00	0.28	0.00	0.02	0.00	0.00	0.98	0.00	0.00	0.75	4	0.50	0.50
Cayo Lobos	0.08	0	0.00	0.20	0.03	0.02	0.75	0.10	0.10	0.15	0.00	0.00	0.25	3	1.00	0.18
Congo Cay 1	0.08	0	0.50	0.10	2.10	0.00	0.23	0.01	0.00	0.76	0.00	0.00	0.10	1	1.00	0.18
Congo Cay 2	0.09	0	0.50	0.08	2.00	0.00	0.04	0.42	0.13	0.46	0.00	0.00	0.25	4	1.00	0.32
Outer Brass 1	0.04	0	2.50	0.30	1.16	1.00	0.59	0.07	0.00	0.35	0.00	0.00	0.50	2	1.00	0.32
Outer Brass 2	0.02	0	0.50	0.73	0.35	0.50	0.00	0.10	0.86	0.00	0.00	0.00	0.00	2	1.00	1.00
Salt Cay 1	0.11	0	0.33	0.10	0.42	0.16	0.90	0.10	0.00	0.00	0.00	0.00	1.00	5	1.00	1.00
Salt Cay 2	0.18	0	0.67	0.05	0.84	0.08	0.00	1.00	1.00	0.00	0.00	0.00	0.50	1	1.00	0.67
Isla Mona 1	0.02	0	0.00	0.21	0.58	0.00	0.14	0.15	0.00	0.71	0.00	0.00	1.00	5	1.00	0.67
Isla Mona 2	0.02	1	0.00	0.11	0.25	0.00	0.58	0.07	0.10	0.25	0.00	0.00	0.75	3	1.00	0.42
Gt. St. James 1	0.06	0	0.50	0.10	0.58	0.00	0.58	0.29	0.00	0.00	0.00	0.13	0.25	1	1.00	0.42
Gt. St. James 2	0.05	0	1.00	0.15	0.53	0.00	0.00	0.27	0.00	0.68	0.00	0.05	0.25	3	1.00	0.42
Gt. St. James 3	0.05	0	0.35	0.15	0.00	0.00	0.27	0.45	0.00	0.24	0.00	0.04	0.50	4	1.00	0.50
Buck Is. 1	0.04	0	0.00	0.00	0.50	0.00	0.28	0.06	0.00	0.66	0.00	0.00	1.00	4	1.00	0.50
Buck Is. 2	0.13	0	0.33	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.25	2	0.50	0.50
Buck Is. 3	0.10	0	0.33	0.00	0.05	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	2	0.25	0.50
Steven Cay	0.00	0	0.00	0.01	2.79	0.00	0.16	0.08	0.00	0.76	0.00	0.00	1.00	3	1.00	1.26
Saba Cay	0.00	0	2.00	0.00	1.06	0.00	0.08	0.08	0.00	0.84	0.00	0.00	1.00	2	1.00	1.02
Cas Cay	0.04	0.00	0.00	0.0476	0.12	0.00	0.78	0.09	0.00	0.13	0.00	0.00	1.00	3	1.00	1.40

¹See appendix A for variable descriptions.

inhabiting rat free islands. ANOVA performed on the regression line ($y = -5.548x + 1.127$) which plots *Anolis* perch height vs. rat density on my study islands (Tolson and Campbell in prep) shows a negative correlation ($p = .0137$) between rat density and *Anolis* perch height. This is not surprising. *Anolis cristatellus* resident on rat-infested islands exhibit a typical escape behavior. Male Puerto Rican *A. cristatellus* escape to the canopy when threatened (Heatwole 1968), but those on Congo Cay, Outer Brass, and Salt Cay all run to the ground when disturbed, even when suitable cover on the ground is lacking. At night, the *Anolis* are not usually found sleeping exposed on vegetation, but rather under rocks. This is extremely unusual behavior for *A. cristatellus* (E. Williams pers. comm.).

Although one does not often discover *E. monensis* on islands which are infested with rats, some sympatry does occur. Isla Mona and St. Thomas are islands with moderate rat densities and extant (although apparently dwindling) populations of *E. monensis*. Interestingly, at localities where *Epicrates* coexists with *Rattus*, there are also significant numbers of introduced mammalian predators such as *Felis* and *Herpestes* (table 2).

Discussion

PCA and *E. monensis* Habitat Utilization

The Puerto Rico Bank encompasses a total land area in excess of 9,300 km², of which 1700+ km² (or 17.6%) is covered with subtropical dry forest (Ewel and Whitmore, 1973). This xeric forest is widely distributed throughout the range of *Epicrates monensis*, yet the boa, as far as we know, occupies only seven islands of the 243 that make up the banks—effectively exploiting only 0.04% of the land area available to it. PCA helped to identify those factors which seem

to define critical boa habitat. Several vegetative parameters which cluster together in the PCA are descriptive of habitat where I or others have encountered *E. monensis* repeatedly. These include areas with high shrub and palm densities coupled with a low canopy and vegetational continuity. These values describe plot habitat on Diablo 2, Icacos 2, and certain sites within the Red Hook area of St. Thomas. Either high shrub or high palm densities coupled with vegetational continuity and lower canopy are found on Diablo 3, Icacos 3, and Mona 1. Of these two subsets of PC I, boas occur on Diablo 2 and 3, Mona 1, St. Thomas, and almost certainly inhabited Icacos 1 and 3 at one time.

In PC II, habitat correlates include high compound tree density, high canopy height, vegetational continuity, and low grass density. This is a perfect structural and compositional description of Diablo 1, which has the highest population of *E. monensis* I have ever encountered, and Mona 2—another locality where *E. monensis* has been observed (Campbell and Thompson 1978). It seems clear from these data that the unifying variable which causes an intersection of these two differing habitat types is vegetational continuity—an interlocking of the branches of shrubs or the tree canopy. I believe this vegetational characteristic is essential to *E. monensis* foraging success and survival. It probably not only decreases the search time between encounters with sleeping *Anolis* while foraging, but it also potentially limits the encounters between the boa and *Felis* and *Herpestes*. Fortunately, at least some tracts of subtropical dry forest and *Coccoloba* have remained relatively undisturbed on the Virgin Islands, Isla Mona, and Puerto Rico and its offshore satellites. Much suitable habitat does exist—even near populated areas.

While habitats throughout the Bank are presumably underutilized by *E. monensis*, and suitable areas for

reintroduction apparently exist in a number of localities, the extant boa populations are so fragmented and reduced in numbers that it is crucial to protect those areas now supporting the boa. This may be difficult. Historically, vegetation on Puerto Rico and the Virgin Islands has been severely disrupted, and 17th-18th century land use patterns on the U.S. Virgin Islands may partially explain the limited distribution of the boa on the east end of St. Thomas and its absence from St. John. Even now enormous pressures exist for continued development on the east end of St. Thomas. Construction around Red Hook seems to have accelerated in recent months, perhaps in response to the decline of interest rates in the United States, and three relatively undeveloped areas on the east end—Red Hook Mountain, Cabrita Point, and Water Point—all have projects in progress that do not involve federal funding. The management authority on St. Thomas, U.S. Virgin Islands—the Division of Fish and Wildlife—has no control over such development.

In contrast, Puerto Rican islands with populations of *Epicrates monensis* are in no imminent danger of development. Cayo Diablo is part of the Reserva Forestal de La Cordillera, and Isla Mona is likewise a Forest Preserve (although it was once proposed to develop the island as a deep-water oil port). A problem does exist, however, with habitat destruction on isolated cays caused by campers and fishermen (Heatwole and Mackenzie 1967). *Coccoloba* trees in the larger groves—areas where the greatest densities of *E. monensis* are found—are often used as firewood by visitors. A survey done in 1987 of damage to *Coccoloba* stands on Cayo Diablo showed that many trees sustained some sort of damage caused by human activity, primarily machete cuts and burns from fires started at the bases of the trees.

Effects of Feral Mammals

My analysis shows that *Rattus* and *Felis* are a primary influence on community composition on the Puerto Rico Bank. *Felis* presence is associated with low *Alsophis*, *Margarops*, and *Rattus* density (table 1: PC I); *Felis* absence is associated high *Anolis* and *Alsophis* densities in PC IV (table 1). Clearly the presence of *Felis* in *E. monensis* habitat is a mixed blessing. Cats present a great danger to *Epicrates* because they hunt at night. Several instances of cat predation of *Epicrates* have been reported on St. Thomas (D. Nellis pers. comm.) In fact, in April and May of 1988 two *E. monensis* were rescued from cats on St. Thomas and were incorporated into the captive breeding program at the Toledo Zoological Gardens. In contrast, however, on islands where boas and rats coexist—Isla Mona and St. Thomas—there are also significant populations of *Felis*. Cats feed on *Rattus* and may keep rat populations at levels low enough to permit survival of the boa. Their apparent adverse affect on *Alsophis* and *Margarops* density—two potential predators of *E. monensis*—may also be of some small benefit in certain circumstances. Weiwand's (1977) observation of cat predation of *Alsophis* on Isla Mona corroborate the PC I linkage of cat presence with low *Alsophis* density.

I cannot be certain whether *Rattus* affect boa populations by acting primarily as a constraint on their resource levels or by direct predation. Although I have been unable to demonstrate that rats forage on boas, I have every reason to suspect that they do. *Rattus* is known to prey on lizards (Whitaker 1978). While surveying for boa populations on the Bank I found habitat (Congo Cay, Outer Brass Cay) which provides optimal foraging opportunities for the boa (e.g. vegetation associated with population densities of > 60 *Anolis*/100 m² on rat-free islands) but had no or few boas and were virtually over-

run with rats at night. Rats may also affect boa populations by preying on *Anolis* directly or by influencing their perching behavior, (indicated by the negative correlation between rat density and *Anolis* perch height (table 1: PC I) or selection of sleeping sites. If lizards rarely rest in the canopy at night but rather seek refuge sites on the ground, there would be potentially disastrous consequences for boa foraging success. *Rattus* also apparently affect *Margarops* density (table 1: PC V).

There can be little doubt that the Indian mongoose, *Herpestes auropunctatus*, threatens *Epicrates monensis* directly as well, but I believe the risk to *Epicrates* is sometimes exaggerated. *Herpestes* predation on endemic West Indian snakes is well documented (Maclean 1982), but the mongoose is a strictly diurnal, terrestrial predator; *Epicrates monensis* is nocturnal and arboreal. *Herpestes* poses the greatest danger to the diurnal West Indian racers, genus *Alsophis*, and are directly responsible for the extinction of *Alsophis sancticrucis* on St Croix and the extirpation of *A. portoricensis* from St. Thomas and St. John. In contrast, I have found *Epicrates monensis* abroad during the daylight hours on only two occasions over a period of several years. It seems that *Herpestes* would have the greatest chance of capturing *Epicrates* when the latter is resting in some moderately accessible location during the day—in loose sections of termite nests, for example. Feral pigs (*Sus scrofa*) may also threaten the Mona boa to some degree, either by eating them or by destroying vegetation, such as terrestrial bromeliads, that may act as snake refugia. I have no data on the magnitude of this threat.

Natural Predators

The Puerto Rico Bank has no extant species of native mammalian predators, but two nocturnal avian predatory species may pose a limited

threat to *Epicrates monensis*. The yellow-crowned night heron, *Nyctanassa violacea*, and the Puerto Rican screech owl, *Otus nudipes*, are two potential predators of the boa. While populations of *Otus* are declining on the bank (IUCN 1981) those of the heron seem quite stable. I have repeatedly observed herons foraging at night in boa habitat on both Isla Mona and Cayo Diablo. Examination of the debris beneath heron rookeries on Cayo Diablo has revealed numerous fragments of *Anolis* and *Ameiva* skin and skeletal materials, usually ribs, vertebrae, and jaw elements. No snake remains have been found, but my co-workers and I are continuing to investigate this potential problem. I also found that *Anolis* densities and perch heights are reduced (table 2) on plots with high pearly-eyed thrasher densities. In PC I (table 1) high *Anolis* perch heights are associated with low thrasher density. These birds also prey on *Anolis*, and are so common in some areas they could easily depress *Anolis* population numbers. Principal component VI (table 1) couples high thrasher density with low *Anolis* density.

Two arthropods are potential predators of *E. monensis*: the land crab *Gecarcinus* and the hermit crab *Caenobita clypeatus*. Searches of terrestrial refugia for *Epicrates* have revealed that these snakes are nearly always absent from areas occupied by *Gecarcinus* and *Caenobita*. This is especially true in termite nests. Snakes only occupy areas of the nest that are inaccessible to crabs. If weathering or disturbance causes a section of termite nest to become habitable for crabs it is abandoned by *Epicrates*, despite their prior use of the refugium for several past field seasons. In hundreds of examinations of refugia over the past five field seasons, I found *Epicrates* in association with *Caenobita* on only one occasion: I found a gravid female thermoregulating under a discarded tarpaulin in the midst of several *Caenobita* on 7 September 1987. Evidence for preda-

tion by the aforementioned species is strictly circumstantial, but the fact remains that over 17% of the *Epicrates* captured have obvious wounds, scars, or partially amputated tails. This is strong evidence that some form of natural predation is occurring.

Climatic/Stochastic Events

The apparent extirpation of the snake from the majority of the islands on the Bank relate not only to the arrival of European man on the Bank and the habitat destruction which followed, but also to climatic, eustatic, and stochastic events, many of which had profound influences on habitat. During the late Pleistocene several climatic and eustatic events occurred that apparently set the stage for the decline of *E. monensis* on the Bank. Foremost among these was a dramatic change in the climate of Puerto Rico. From a relatively xeric climate, Puerto Rico became progressively more mesic during the late Pleistocene. Today, over 81% of Puerto Rico's vegetation is classified as moist or wet forest (Ewel and Whitmore 1973). Pregill (1981) and Pregill and Olson (1982) describe the effect this climatic change had on the xeric-adapted Puerto Rican herpetofauna. This extreme climatic shift may have resulted in the extirpation of *E. monensis* on Puerto Rico.⁴ In addition, sea levels rose nearly 100 m about 8,000-10,000 years ago and separated the Virgin Islands from one another and from Puerto Rico, transforming what was a contiguous land mass into a scattered series of islets and cays spread over nearly 400 km. Many of these cays now have extremely low elevations (Heatwole and Mackenzie 1967).

⁴It is unclear why *E. monensis* is absent from the dry forest in southwestern Puerto Rico. Habitat in the Guanica forest seems quite suitable for the boa; perhaps further survey work will result in its discovery there.

The fragmentation of *E. monensis* into several small demes may have left several populations without the genetic resources to survive changing environments, and doubtless allowed stochastic processes such as disease, prey fluctuations, or storms to extirpate many isolated populations. I assume that the influences of random events on the present distribution of the native herpetofauna complicates the multivariate analysis by introducing more variance into the correlation matrix. These factors may explain the absence of snakes from islets with suitable habitat, as some of these islands may have inadequate food resources or lower probabilities of recolonization.

Management Recommendations

The forces threatening *Epicrates monensis* are complex. Solutions for the recovery of the boa will not be simple, but I am optimistic about the chances of success. My management recommendations are summarized below.

Saving Boa Habitat

This may be impossible on St. Thomas, but with luck the boa may coexist with man (as it now does) at some relatively developed localities. Continued protection of Isla Mona and La Cordillera are absolutely necessary.

Continued protection and management should be extended to those cays now protected by the Division of Fish and Wildlife, U.S. Virgin Islands—particularly Congo Cay, Outer Brass Cay, Salt Cay, Savana Island and Steven Cay—as these sites might eventually be utilized for reintroduction programs. The smaller islands should be off limits to casual visitors to prevent habitat damage and human persecution of the snakes.

Predator Eradication on Suitable Offshore Islets

Rat control programs should be initiated immediately on those islands with habitat suitable for *E. monensis*. Preliminary studies of rat eradication using anticoagulant poisons on some small cays near St. Thomas have produced promising results (Division of Fish and Wildlife, USVI 1983). It is critical, however, that time and funding be committed for follow up studies on any islands made the subject for a rat control program. This must be done to ensure that immunity to poisons has not evolved or that populations are being replenished by recolonization from St. Thomas.

It is unlikely that *Felis* or *Herpestes* will ever be eradicated from larger islands such as Isla Mona or St. Thomas, but *Felis* control programs now in force on Mona should be continued to further reduce populations and should be expanded to include Cayo Icacos. It is important to convince management authorities that feral mammal control measures on the Bank must be increased, and quickly.

It is a credit to the evolutionary resilience of this little snake that it has survived at all. Few endangered species have been exposed to such a wide range of adverse effects and have still survived. It is my fervent hope that this, and other endemic species of the Caribbean, will not be exterminated in the wake of the living human debris, such as *Rattus rattus*, that we have allowed to pollute the islands of the West Indies.

Captive Breeding for Reintroduction Purposes

Captive propagation can figure significantly in the recovery of this snake (USFWS 1986). The current cooperative breeding plan for *E. monensis* should be expanded to more American Association of Zoological Parks and Aquarium member institu-

tions, and Species Survival Plan designation should be sought for the snake immediately to facilitate genetic management of the captive population.

For the present, until genetic analysis has been completed, the strategy of deme integrity maintenance should be continued, with St. Thomas founders and La Cordillera founders managed as separate populations. Continuous outcrossing within demes facilitated by a random pair mating scheme should be encouraged. Fortunately, the first captive breeding has already taken place, the proximate factors critical to reproduction have been identified (Tolson and Tuebner 1987), and there is no reason why the captive population cannot be expanded quickly for reintroduction attempts within five years.

I firmly believe that we are finally at the point where we can look forward to augmenting boa populations, rather than helplessly watch them decline.

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Appendix A.

PCA Variables Measured on Island Study Plots.

Variable	Description
Predator	
<i>Rattus</i> density	Rats captured/trap hour
<i>Felis</i> presence	Present = 1, absent = 0
<i>Alsophis</i> density	Mean no. <i>Alsophis</i> observed/day on transect
<i>Margarops</i> density	Mean no. <i>Margarops</i> observed/day on transect
Prey	
<i>Anolis</i> density	Mean no. <i>Anolis</i> /5 m of transect
<i>Ameiva</i> density	Mean no. <i>Ameiva</i> /5 m of transect
<i>Anolis</i> perch height	Mean perch height in m of male <i>Anolis</i>
Coverage	
Percent cover C trees	No. compound trees/no. woody plants
Percent cover S trees	No. single trees/no. woody plants
Percent cover palms	No. palms/no. woody plants
Percent cover Opuntia	No. Opuntia/no. woody plants
Percent cover grasses	Grassland area/total area
Structural	
Vegetational continuity	Contiguous = 1, high = .75, Moderate = .5 low = .25, absent = 0
Canopy height	>3 m = 1, 1-2 m = .5, <1 m = 0
Plant diversity	No. of dominant plant species on plot

The Use of Timed Fixed-Area Plots and a Mark-Recapture Technique in Assessing Riparian Garter Snake Populations¹

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Abstract.—Wandering garter snake (*Thamnophis elegans vagrans*) populations along a thin-leaf alder (*Alnus tenuifolia*) riparian community in northern New Mexico were sampled using timed fixed-area plots and a mark-recapture method. Both methods served to determine yearly differences and relative magnitude of snake density between years. But population estimates determined by timed fixed-area plots were inconsistent between study plots in the same year.

Research studies often attempt to determine the effects of disturbance or management regimes on the abundance of wildlife species (Cooper-rider et al. 1986, Fitch 1987, Parker and Plummer 1987, Ralph and Scott 1980). How well the method of data collection and analyses reflect actual populations is critically important for assessing the validity of these studies. Snakes are difficult subjects for field studies because of their secretive and cryptic habits (Fitch 1987).

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Many attempts to census snakes have been inaccurate (Turner 1977, Fitch 1987). Population estimates can be influenced by sex, reproductive condition, and stage of maturity, all of which are critical determinants of activity within species (Gibbons and Semlitsch 1987). Differences among juveniles and breeding and non-breeding females, and males often lead to much different risks of capture at various stages of the season and time of day. Overall population estimates can be distorted as a result, requiring separate estimates by sex and age class (Fitch 1987).

Two methods often used to estimate snake density are direct counts and mark-recapture analyses. Systematic searches of defined areas (direct counts) yield species occurrence data, and usually require less time and effort than mark-recapture methods (Jones 1986). Using direct counts, Bury and Luckenbach (1977) successfully censused desert tortoise (*Gopherus agassizii*) populations with a quartet and grid location system. Bury (1982) used a removal method to assess reptile community structure in the Mohave Desert (Zippin 1956, 1958). Bury and Raphael (1983) refer to searches conducted per unit effort of time as time-constraint procedures. Usually it is impossible to find every snake in an area, making it necessary to estimate population size

from capture-recapture ratios (Fitch 1987). Yet, when several density estimates become available from the same area at different times, they often show such drastic discrepancies that the basic methods have been thought invalid (Turner 1977). Turner (1977) had no confidence in the density estimates for snakes derived from mark-recapture techniques. However, since his critical review, estimation techniques have greatly improved with the development of models and computer programs that test model assumptions and estimate standard errors (Arnason and Baniuk 1980, White et al. 1978, 1982, Otis et al. 1978, Brownie et al. 1985).

Although time consuming, determining accurate population estimates is necessary to develop management policies not only for abundant species, such as the wandering garter snake (*Thamnophis elegans vagrans*), but also for aquatic or semi-aquatic endangered snake species such as the Concho water snake (*Nerodia harteri paucimaculata*) (Scott and Fitzgerald 1985) and the narrow-headed garter snake (*Thamnophis rufipunctatus*) (Lowe 1985). However, because the wandering garter snake, is less secretive than most kinds of snakes, and is concentrated in riparian habitats, it is probably one of the best adapted to this sort of investigation (Fitch, per-

sonal communication). The results of this work should be directly applicable to other snake species normally concentrated in riparian ecosystems and may be especially useful for censusing endangered species where large samples to determine the accuracy of sampling techniques are not available. Our previous work showed the inadequacy of simple transects and depletion sampling in determining garter snake populations along the Rio de las Vacas, New Mexico (Szaro et al. 1985). The objective of this study was to compare timed fixed-area plots and a mark-recapture technique in assessing the impacts of management regimes on riparian ecosystems in the arid Southwest by sampling wandering garter snake populations along the Rio de las Vacas.

Methods and Study Areas

The Rio de las Vacas, is a montane stream draining the San Pedro Parks Wilderness Area, Santa Fe National Forest, New Mexico. Under low flow conditions, stream width ranges from 2.8 to 10.5 m and averages 7.6 m. The study area is 17 km southeast of Cuba, in Sandoval County, at 2600 m. Two cattle exclosures enclosing stream reaches (each about 1 km long by 50 m wide) were installed in the early 1970's (Szaro et al. 1985). Contiguous, downstream areas, privately owned and grazed by livestock, were used for comparison. The most apparent difference between the grazed and exclosed stream segments was the band of small riparian trees and shrubs in the exclosures (figs. 1 and 2). Thin-leaved alder (*Alnus tenuifolia*) and a mixture of willow species (*Salix* spp.) edged the exclosure streambanks but were widely scattered where the streambanks were grazed (9.5 ± 1.16 , 7.5 ± 1.23 , and 0.3 ± 0.14 trees/250 m² in exclosures 1, 2, and grazed areas, respectively).

Snake populations were estimated by timed fixed-area plot sampling,



Figure 1.—Grazed section of the Rio de las Vacas, New Mexico. Notice the lack of shrub growth and the unstable stream banks.

and mark-recapture sampling in both grazed and ungrazed areas. For the former, 16 plots (10 x 25 m), with the long edge being defined by the stream bank, were intensively sampled for 20 minutes in each of the

two ungrazed exclosures and one grazed stream segment along the Rio de las Vacas, for a total of 48 plots (fig. 3). During sample periods we turned rocks, logs, debris piles, and generally searched the area. All plots



Figure 2.—Shrubby growth in Exclosure 2 along the Rio de las Vacas, New Mexico.

were sampled once between 0900 and 1300 hours (MST) within a 3-day period each month. Sampling times were determined from preliminary activity period sampling that showed two distinct periods of activity (morning and late afternoon). All snakes captured were placed in a cloth sack at their point of capture, until the end of the sampling period. Plot sampling began in June 1984 and was replicated in July, August, and September of that year and in the same months in 1985. Total time spent sampling was approximately 64 hours per year, excluding time between samples to process snakes.

For mark-recapture estimates, we searched the entire extent of both exclosures and a similarly sized downstream grazed stream area. The plots used for the timed-fixed plot sampling were a subset of the area used for the mark-recapture sampling. All captured snakes were marked by clipping three subcaudal scales (Blanchard and Finster 1933, Woodbury 1956). Mark-recapture sampling periods occurred in the same months as the plot sampling; but snakes were captured, marked, and released dur-

ing intensive searches for 6 consecutive days by 3 to 4 collectors. All snakes were released where captured. Approximately equal time and effort was spent searching for snakes in each of the three areas. Time of day bias was minimized by alternating starting areas daily. Sampling began at 0900 hours (MST) and continued until dusk. Only captures within 10 m of the stream were used in the mark-recapture analyses to allow a direct comparison to plot sampling estimates. Thus, the plot sampling represents a sample within the exclosures and the grazed stream area, whereas the mark-recapture sampling represents an "open" population estimate of each study area. Total time spent sampling and marking snakes was approximately 450 hours per year including time to process snakes.

The approach to mark-recapture analysis was to analyze each year separately using closed population models calculated by program CAPTURE, which allows unequal catchability (Otis et al. 1978, White et al. 1978, 1982) as recommended by Pollock (1981, 1982). Because we were

unable to estimate survival using the timed fixed-area plots, we do not present these estimates here for the mark-recapture analysis. However, all sampling periods were pooled and survival estimators between years estimated using the Jolly-Seber Model (Seber 1986, Szaro et al., in preparation).

Inferences about differences between years and exclosures were based on Bonferroni's method for multiple comparisons by fixing the experimentwise error rate at 0.05 (Milliken and Johnson 1984). Thus, the overall experimentwise error rate is less than P (in this case 0.05); but for each comparison, the comparisonwise error rate is equal to P/n , where n is the number of comparisons. For example, with 3 comparisons the actual P value per comparison would be $0.05/3$ or 0.017.

Results

We are confident the mark-recapture estimates accurately reflect population densities on the three study areas and use these as the basis for

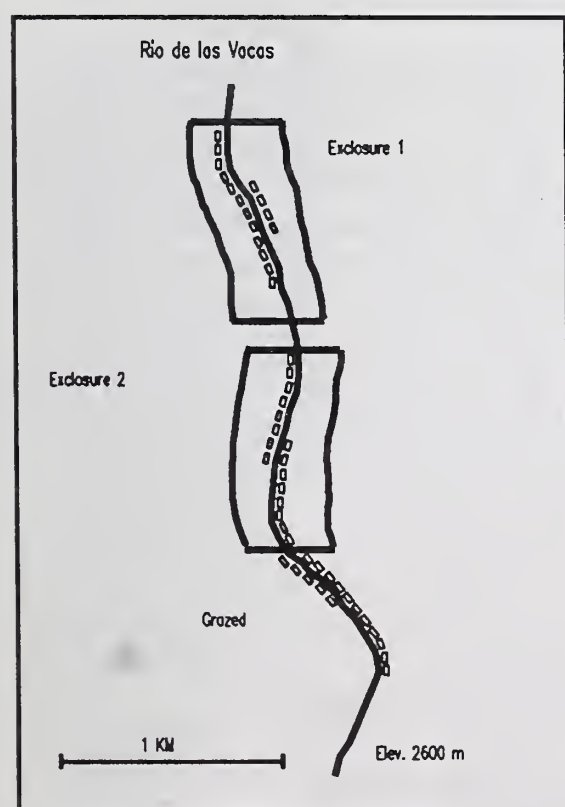


Figure 3.—Study areas and sample plot layout along the Rio de las Vacas, New Mexico.

Table 1.—Population estimates of the wandering garter snake (*Thamnophis elegans vagrans*) in 1984 and 1985 within 10 m of the streambank at Rio de las Vacas, New Mexico.

Study area	Year	Mark-recapture ¹			Times fixed-area plot ²		
		Mean	S.E.	Sig. ³	Mean	S.E.	Sig.
Exclosure 1	1984	282 ± 23.53	(3.86) ⁴	a	1.28 ± 0.18		a
	1985	166 ± 15.51	(2.28)	b	0.88 ± 0.11		a
Exclosure 2	1984	296 ± 24.42	(4.53)	a	1.30 ± 0.17		a
	1985	146 ± 13.92	(2.23)	b	0.45 ± 0.09		c
Grazed	1984	67 ± 10.49	(1.00)	c	0.28 ± 0.07		cd
	1985	26 ± 5.22	(0.39)	d	0.11 ± 0.04		d

¹Mark-recapture estimates for each study area are for the total population using the best model in CAPTURE for which solutions exist. The total area sampled in each area was 18,240 m² in Exclosure 1, 16,340 m² in Exclosure 2, and 16,760 m² in the grazed area.

²Plot samples are mean number of snakes caught per 250 m².

³Population estimates by each method that do not have a letter in common are significantly different (Bonferroni's method, $P \leq 0.05$).

⁴Number in parenthesis is estimated number of snakes per 250 m² using the mark-recapture population estimate.

comparison for the timed fixed-area plot results. Mark-recapture estimates were based on 118 individuals and 35 recaptures (118/35) in enclosure 1 in 1984, 72/28 in 1985, 127/30 in enclosure 2 in 1984, 74/26 in 1985, 12/2 in the grazed area in 1984, and 10/1 in 1985.

We asked two questions of the sampling methods. First, were there any differences in population estimates between years? Both methods indicated decreases in population size on all three areas between 1984 and 1985. However, yearly differences were significant only for mark-recapture estimates and for the timed fixed-area plot estimates in enclosure 2 ($P \leq 0.05$) (table 1). Mark-recapture estimates revealed that snake populations decreased by 41% to 54% from 1984 to 1985 in all study areas. Decreases in mean number of snakes per fixed-area plot were not as uniform, varying from 31% on enclosure 1 to 65% on enclosure 2 and the grazed stream segment.

Second, were there differences between the study areas? Population estimates between enclosures and the grazed stream segment within a given year were significantly different by both census methods and for both years ($P \leq 0.05$) (table 1). Population estimates by both methods were not significantly different between enclosures, except in 1985 when the estimate determined by timed fixed-area plots for enclosure 2 was 50% of that on enclosure 1 ($P \leq 0.05$) (table 1).

Estimating population size by restricting the mark-recapture estimates to a 10 m band on either side of the stream served a twofold purpose. First, it allowed us to estimate the number of snakes per unit area. Second, it made estimates by both techniques more readily comparable, because all plot sampling was confined to the 10-m band next to the stream where most of the available down litter, grass clumps, and shrubby vegetation was concentrated. In enclosure 1, there were 3.86

and 2.28 snakes per 250 m² in 1984 and 1985, respectively. In enclosure 2, there were 4.53 and 2.23 snakes per 250 m² in 1984 and 1985, respectively. Along the grazed stream reach there were 1.00 and 0.38 snakes per 250 m² in 1984 and 1985, respectively. Based on these estimates, we caught between 20.2% (enclosure 2, 1985) and 38.6% (enclosure 1, 1985) of the snakes present in the enclosures. On the grazed area we caught 28% of the snakes in both 1984 and 1985.

Discussion

Apparent short-term downward population fluctuations averaging about 50% have been found in several mark-recapture studies (Fukada 1969, Platt 1969, Fitch 1975, Feaver 1977, Gregory 1977). Many studies of snakes have related population changes over several years to successional changes (Clark 1970, Fitch 1982) or to environmental factors, such as decreases in annual precipitation (Clark 1974, Clark and Fleet 1976). Another possibility, is that a study like this actually destroys hiding places (turning rocks, logs, etc.); and even if each piece is put back carefully, the site has opened up and changed (Clark, personal communication).

We undoubtedly had some impact on the quality of the available habitat by our intensive searching tactics; but we did try to be as careful as possible to return moved objects back into their original positions. Parker and Plummer (1987) suggest that these apparent fluctuations in density result from changes in activity level (which affect recapture probabilities) rather than from actual changes in density (Lillywhite 1982, Pough 1983). There are three possible explanations for these results: (1) snakes simply moved out of the plot and enclosure areas; (2) snakes became inactive in burrows or cover sites because of environmental conditions; or (3) snakes died.

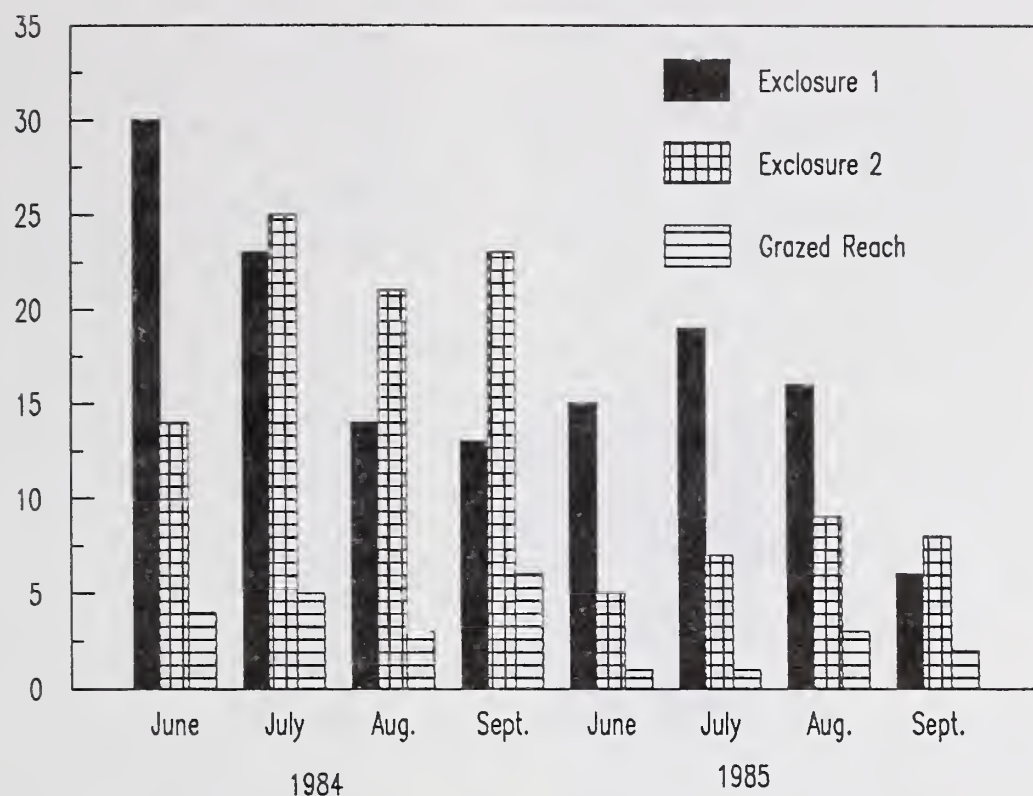
Activity periods of wandering garter snakes varied between individuals from our preliminary sample of wandering garter snake populations along the Rio de las Vacas in July 1983. We failed to decrease significantly the total numbers of animals caught per plot even after 3 days of removal sampling (Szaro et al. 1985); but at other times snakes were difficult to find. However, we feel the intensive sampling effort of at least 1 week each month minimized the effect of changes in snake behavior on population estimates.

The almost 50% difference in 1985 between enclosures in mean number of snakes caught while plot sampling was probably a result of a shift in areas used by the snakes and not differences in mortality between the two enclosures. Monthly trends in total number of snakes caught also showed a dramatic difference in the number of snakes caught per month while plot sampling in both enclosures. However, this difference was not reflected in the overall number of snakes caught during mark-recapture sampling (fig. 4). In fact, overall we caught more snakes in enclosure 2 than in enclosure 1 in all months in 1985.

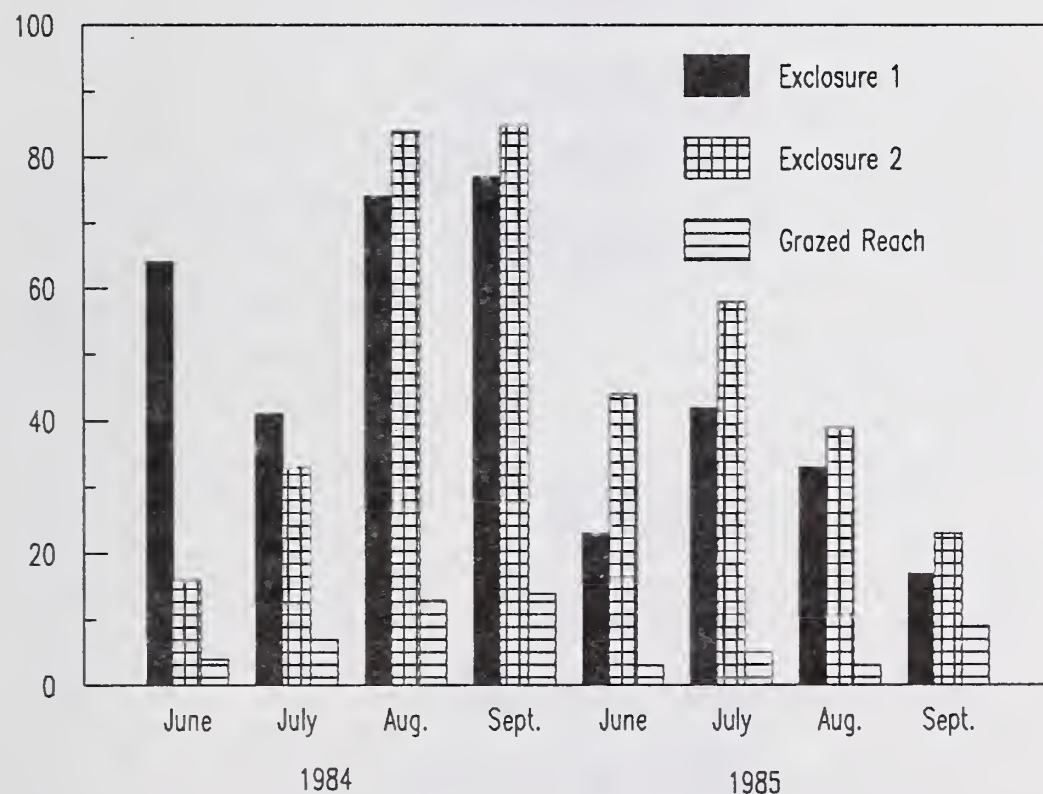
The difference in plot sampling estimates between enclosures in 1985 was not a result of changes in daily activity patterns, because equal proportions of snake captures in both enclosures were before 1300 (63% in enclosure 1 and 59% in enclosure 2, chi-square, $P > 0.05$). Furthermore, differences in captures between years and methods were not sex-based, because there were no significant differences in sex ratios between years or method in a given study section (chi-square, $P > 0.05$) (fig. 5). However, there were distributional differences in snake captures between years and enclosures.

In 1984, 34.6% and 34.7% of all captures on enclosures 1 and 2, respectively were made on the plot areas. In contrast, 42.1% and 20.6% of all captures on enclosures 1 and 2, re-

Plot Sampling



Mark-Recapture Sampling



Sampling Period

Figure 4.—Total numbers of wandering garter snakes caught in June, July, August, and September 1984 and 1985 along the Rio de las Vacas, New Mexico during timed fixed-area plot and mark-recapture sampling.

spectively, were made on the plot areas in 1985.

We cannot explain this distributional shift in exclosure 2. Although we did not plot sample in 1986 and 1987, mark-recapture efforts in those years showed a similar distributional pattern (Szaro et al., unpublished). In exclosure 1, 33.0 % and 37.3% of all captures in 1986 and 1987, respectively were on the old plot areas, whereas in exclosure 2, these values were 10.0% and 9.8%.

We feel that the distributional changes in exclosure 2 were not an artifact of plot sampling, because snakes in exclosure 2 did not return to plot areas after plot sampling had stopped. In any case, our sampling potentially would have been more destructive in exclosure 1 than in exclosure 2 because of the higher incidence of turnable rocks in that exclosure.

Whatever the cause, these changes in distribution indicate that initial randomized selection of plots did influence density estimates for exclosure 2. Although it would increase substantially the amount of time necessary to adequately sample vegetation, a better approach would be to randomly select plots within exclosures each sampling period rather than repeatedly sampling the same plots.

In conclusion, the use of timed fixed-area plots enabled us to quantify dramatic differences in snake abundance between exclosures and the grazed area. However, this sampling method is of questionable merit because of the significant difference in exclosure population estimates for 1985. Further study incorporating newly randomized plots for each sampling period may solve this problem. Care should be taken to determine if snakes are distributing themselves in a nonrandom pattern. At this time, we recommend the more labor-intensive mark-recapture estimators for assessing the impacts of riparian management regimes on snake populations.

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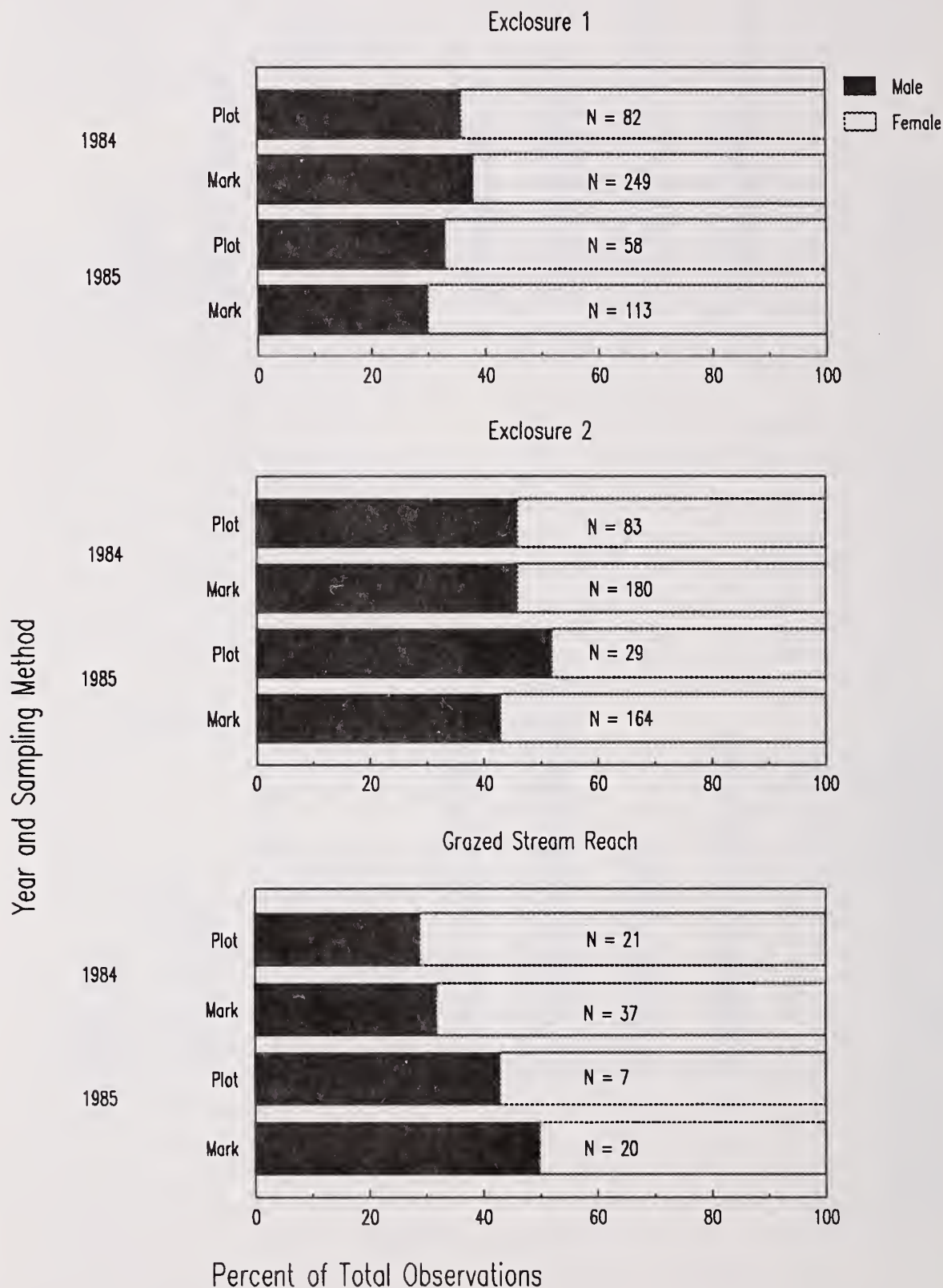


Figure 5.—Proportion of total captures by sex during timed fixed-area plot and mark-recapture sampling in two exclosures and a grazed stream reach along the Rio de las Vacas, New Mexico, 1984 and 1985.

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Design Considerations for the Study of Amphibians, Reptiles, and Small Mammals in California's Oak Woodlands: Temporal and Spatial Patterns¹

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The hardwood rangelands of California are coming under increasing land-use pressures. Cattle grazing, fuelwood removal, hydro-electric projects, urban sprawl, and countless other factors are impacting these woodlands at local, regional, and geographical levels (see papers within Plumb and Pillsbury 1987). Unfortunately, little is known of the distributions and ecologies of many of the vertebrates occurring in these areas (Verner 1987). As a consequence, resource managers frequently have too little information upon which to base land-use decisions. Thus, a research agenda is required first to obtain baseline information on distributions and habitat associations of these animals, and then to use these data to predict the presence or absence of these species, and ultimately to predict the effects of habitat change on their populations. Research should encompass a hierarchy of spatial scales to account for variations in patterns of habitat use, and also to determine if a species' habitat exhibits consistent and measurable features (Allen and Starr 1982, Block, in press). Study must

also be done year-round to sample habitat-use by species during different stages of their life histories, and it also should be done over a number of years to include annual variations in environmental conditions (Halverson 1984, Morrison, this volume).

As part of an ongoing study to determine habitat relationships of vertebrates in California's oak woodlands, we have been using pitfall traps to sample populations of small mammals, reptiles, and amphibians at three distinct areas. To date we have collected data from greater than 50,000 trap nights distributed among 20 trapping grids. This general design has allowed us to examine spatial patterns of habitat-use both within and among areas. Further, more intensive study has been done at one area to examine temporal patterns in habitat use both within and between years. In this paper we present these data to examine spatial and temporal patterns of habitat use and discuss our results in relation to the general design of studies of small mammal, reptile, and amphibian populations.

STUDY AREAS

The study was done at three areas, all oak or pine-oak woodlands. Study areas were distributed along a latitudinal gradient of about 600 km, and consequently there were notable differences in topography and in com-

Abstract.—We monitored pitfall traps for >50,000 trap nights among three study areas in California's oak woodlands. Numbers of captures and trap success varied spatially in comparisons of grids within and among stand types, as well as among study areas. Capture numbers also varied temporally, both within and between the years of study. Differences in capture rates varied among taxa (amphibians, reptiles, and small mammals) and also varied among species within a taxon. Researchers should design studies to sample temporal and spatial variations in activity patterns to provide a more complete understanding of the habitat associations of the species studied.

position and structure of the vegetation among the study areas.

Sierra Foothill Range Field Station (SFRFS), Yuba County, was located in the foothills of the Sierra Nevada about 25 km NE of Marysville. Elevation ranged from 200 to 700 m on a general west-northwest facing slope. Blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and digger pine (*Pinus sabiniana*) were the major species of trees with lesser amounts of California black oak (*Q. kelloggii*), California buckeye (*Aesculus californicus*), and ponderosa pine (*Pinus ponderosa*). Major components of the shrub layer included buckbrush (*Ceanothus cuneatus*), coffeeberry (*Rhamnus californica*), and poison oak (*Toxicodendron diversiloba*). Annual and perennial grasses and forbs dominated cover within a meter of the ground, although there were spatial and temporal variations in species compositions and also in amount of ground cover. Further, the composition and structure of the canopy, shrub, and ground layers have all been modified by historic land-use practices at the Station. Except for 60 ha of fenced areas, the remaining 1800 ha are used for varied research projects usually entailing cattle grazing and often entailing tree removal.

San Joaquin Experimental Range (SJER), Madera County, was located in the foothills of the Sierra Nevada about 40 km N of Fresno. Elevation ranged from 200 to 500 m; the aspect was in a general southwest direction.

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Blue oak, interior live oak, and digger pine were the major tree species. These species occurred in mixed-species stands, stands of blue oak woodland, or as blue oak savannas. Annual and perennial forbs and annual grasses dominated the ground layer. About 20 ha of SJER have been fenced to exclude cattle grazing. Cattle grazing on the remaining 1500 ha has resulted in a sparser shrub understory at SJER than of that found at SFRFS (Duncan et al. 1987). Major shrubs include buckbrush, whitethorn ceanothus (*Ceanothus leucodermis*), redberry (*Rhamnus crocea*), coffeeberry, poison oak, and white lupine (*Lupinus alba*). The shrub understory is restricted mostly to widely scattered stands of mature shrubs which have grown above the deer-cattle browse line.

Tejon Ranch (TR), Kern County, was located about 50 km south of Bakersfield in the Tehachapi Mountains. Elevation ranged from 1100 to 1700 m; aspects included all cardinal directions. Major trees found on TR included blue oak, valley oak (*Quercus lobata*), California black oak, interior live oak, canyon live oak (*Q. chrysolepis*), Brewer's oak (*Q. garryana* var. *breweri*), and California buckeye. At lower elevations, these trees generally occurred in pure stands of single species, with mixed-stands of California black, canyon live, interior live, and Brewer's oaks occurring at higher elevations. Buckbrush, redberry, and mountain mahogany (*Cercocarpus betuloides*) were the major shrubs with annual and perennial grasses and forbs comprising the ground canopy. Cattle grazing and fuelwood harvest have modified the composition and structure of the tree, shrub, and herbaceous layers.

METHODS

Field Methods

At TR we placed three grids in each of three different stand types—blue

oak, valley oak, and canyon live oak woodlands—and we placed four grids in four different stands of mixed-oak woodlands (California black, interior live, canyon live, and Brewer's oaks). At SJER we placed four grids, one each in a blue oak and an interior live oak stand, and two in mixed blue oak-interior live oak-digger pine stands. The three grids at SFRFS sampled three stands of mixed blue oak-interior live oak-digger pine woodlands. Selection of stands was not entirely random because we needed to consider accessibility during inclement weather, and possible conflicts with other research projects or with certain management practices (e.g., excessive cattle grazing, fuelwood harvest, road construction) when selecting stands. The actual selection of the grid location within a stand was by a series of random procedures to determine distance of the grid from the stand edge (>100 m from the stand edge to minimize edge effects) and the direction of the grid array.

Each grid consisted of 36 2-gal, plastic buckets arrayed in a 6 x 6 square with 20-m interstation spacings. Buckets were placed within 2 m of each grid point at a suitable trapping location. Buckets were sunk to ground level and left closed (a piece of plywood secured with a rock) for at least one month prior to being opened. This period enabled germination of grasses and forbs to occur thus making the area near the trap appear less disturbed and also allowed small mammals and herpetofauna to become accustomed to the presence of the traps. Traps were opened by propping a plywood lid 5-10 cm above the lip of the bucket using small branches or small rocks and then placing 3-6 cm of water in the bottom of the bucket. Traps were checked once a week and were left open for 1-2 months at a time. We noted the species, date, and trap location of all captures. Dead animals were removed from traps; live animals were removed and relocated to

a similar habitat at least one km from the nearest trapping grid.

We monitored pitfall traps at TR from 4 January to 20 May 1987 and from 10 December 1987 to 20 June 1988. We regarded the first year of monitoring as a pilot study to evaluate and refine our methods. Traps were opened and monitored for 30 days using the methods described above. However, in light of a recent article by Bury and Corn (1987), we increased our trapping period from 30 to 60-65 days per grid. Thus, our design at TR for the second year consisted of opening one grid of each stand type for 60-65 days, closing those, and then opening another set of four grids. We repeated this design three times. We opened the four grids at SJER and the three grids at SFRFS each for 60 days from mid-January through mid-March 1988.

Data Analyses

We compared standardized capture numbers among stand types at TR and among the three study areas (TR, SJER, and SFRFS) to determine general distributional patterns of the animals caught. Capture numbers were standardized by pooling all captures of a species within a stand type or within a study area and dividing this number by the total number of trap nights for each grid within that stand type or study area. We calculated Spearman rank-order coefficients (Marascuilo and McSweeney 1977) to test for differences in rankings of captures of species among stand types at TR and then of captures among the three areas. We tested for species-specific differences in capture rates among stand types and among study areas using Kruskal-Wallis analyses (Marascuilo and McSweeney 1977).

We used log-linear analyses (Fienberg 1980) to determine the sources of variation in trap success within and among years, stand types, and study areas. We used data only for

the presence or absence of a species at each trapping station, regardless of the number of individuals of the species that were captured at the station. Because the number of trap nights varied between grids, we used this variable as a covariate in all analyses to factor out the bias this might have entered in our analyses.

To test for within-year, spatial-temporal patterns, we restricted our analyses to data collected in 1988. Analyses were done for common species (i.e., those for which we had adequate numbers of samples) and taxon variables of mammals, amphibians, and reptiles. We used data from TR to examine seasonal and stand associations of common species of each taxon.

To examine geographic patterns of captures, we compared trap success among the three study areas. Between-year analyses were done by

comparing trap success at TR from 1987 and 1988.

RESULTS

General Patterns

Tejon Ranch

The ranking of species captured in canyon live oak woodlands was not significantly correlated with the rankings of species found in the other woodland types (all r_s values were nonsignificant, $n = 21$, $P > 0.05$). These differences were attributable to a stronger association of amphibians, particularly *Ensatina* and *Batrachoseps* salamanders, with canyon live oak stands than with the other types of woodlands (Kruskal-Wallis Analyses, $df = 2$, $P < 0.10$) (table 1). Differences among stands were also

noted for captures of *Peromyscus maniculatus*, *P. truei*, *Sceloporus occidentalis*, and *Eumeces gilberti*, which were captured more frequently in blue and valley oak stands than in canyon live or mixed-species oak stands (table 1). In comparisons of rankings of taxonomic groups among stand types, we found a significant positive correlation between mixed-species and valley oak stands, but a significant negative correlation between blue and canyon live oak stands (r_s significant, $n = 3$, $P < 0.01$) (fig. 1). All other pair-wise comparisons between stand types were nonsignificant.

All Study Areas

Rankings of captures of species were weakly correlated only between TR and SFRFS ($r_s = 0.37$, $n = 21$, $P = 0.052$); Spearman rank-order correlations were nonsignificant in all other comparisons. Significant differences were found among areas in the capture rates of *Sceloporus occidentalis*, *Eumeces gilberti*, *E. skiltonianus*, *Batrachoseps attenuatus*, *Batrachoseps nigriventris*, and *Ensatina eschscholtzii* (table 2). In contrast, rankings of taxa were significantly correlated between SJER and SFRFS ($r_s = 1.00$, $n = 3$, $P = 1.00$), but nonsignificant ($P > 0.05$) in all other between-area comparisons. The differences were primarily because of differences in capture rates of reptiles and amphibians (fig. 2).

Log-linear Analyses

Trap success at TR for small mammals, reptiles, and amphibians differed with stand type and trapping period (likelihood ratio chi-squares, $P < 0.01$). Similar results were found for the selected common species. In contrast, fewer differences were found between years for captures of amphibians, reptiles, and small mammals. Only captures of reptiles in blue oak stands and captures of

Table 1.—Capture numbers of amphibians, reptiles, and small mammals within four different oak woodland types at Tejon Ranch, Kern County, California from 1 January 1987 through 20 June 1988.

Species	Valley oak (n=7848) ¹	Blue oak (n=8828)	Canyon live oak (n=7848)	Mixed oak (n=8828)
<i>Batrachoseps nigriventris</i> ²			38	3
<i>Ensatina eschscholtzii</i> ²	19		53	13
<i>Rana boylei</i>		1		
<i>Sceloporus occidentalis</i> ²	20	39		31
<i>Eumeces gilberti</i> ²	28	34		4
<i>Gerrhonotus multicarinatus</i>			1	3
<i>Anniella pulchra</i>	1			
<i>Diadophis pulchellus</i>			1	
<i>Peromyscus maniculatus</i> ²	42	10		3
<i>P. boylii</i>	33	20	22	24
<i>P. truei</i> ²	14			6
<i>Perognathus californicus</i>		1	3	
<i>Microtus californicus</i>	2	2	4	1
<i>Thomomys bottae</i>	8	4	2	6
<i>Reithrodontomys megalotis</i>		1		1
<i>Scapanus latimanus</i>			1	1
<i>Sorex ornatus</i>	1		13	6
Total captures	168	112	138	102
Species richness	10	9	10	13

¹Number of trap nights.

²Significant difference ($P < 0.10$) of captures among stand types.

small mammals within valley oak stands were significantly different between years (likelihood ratio chi-squares, $P < 0.01$). We noted significant differences ($P < 0.01$) in capture frequencies of reptiles and amphibians among study areas, but differences were nonsignificant ($P > 0.05$) for captures of small mammals.

DISCUSSION

Intra-year differences in trap success at TR were observed for all common species and taxonomic groups tested. Much of the intra-year variation in trap success was probably because of differences in activity patterns during different times of the year (Welsh 1987). Our results further suggested that activity patterns varied within and among taxa. For example, few reptiles were captured from December through March; capture rates then increased dramatically after March. In contrast, fewer salamanders were caught in December, January, May, and June than were caught during March and April. Similar results emerge when comparing activity patterns of species within a taxon. Thus, activity patterns of a species or of a taxon tend to be somewhat specific to the animal or group studied.

Differences in trap success were not as apparent for interyear comparisons, however. In fact, the only differences that we noted were increases from 1987 to 1988 in trap success for reptiles in blue oak and for mammals in valley oak stands. These results might be interpreted in two ways. First, species compositions are fairly consistent from year to year, or the 2 years of data that we compared were possibly insufficient to detect population or habitat shifts (Halvorson 1984, Morrison, this volume). Undoubtedly, a long-term study is required to determine if these results remain valid with time or if they are an artifact of the sampling period.

Species distributions also varied spatially among the different stand

types at TR and among the three study areas. For example, canyon live oak stands contained more amphibians and fewer reptiles than other types of stands, whereas few amphibians and more reptiles were captured in blue oak stands. Valley oak and mixed-species oak stands contained intermediate numbers of amphibians and reptiles. We also noted differences of captures among grids of the same woodland type. However, given the short duration of this study (2 years to date), these differences may reflect temporal differences between sampling periods more than variation within stand types. Variation was also noted on a broader geographical scale of between study areas.

Pitfall traps are one of many techniques used to sample vertebrate populations (Day et al. 1980). As with each technique, however, pitfall traps are not without limitations (Bury and Corn 1987). Inter- and intraspecific differences in motility, mode of travel, and activity range all

influence the probability of an animal being captured. Because of probable species-specific biases in catchability, a study design should consider alternative methods (e.g., live traps for small mammals, and active searches for reptiles and amphibians) to sample the population(s) of the species of interest (Halvorson 1984, Raphael and Rosenberg 1983, Welsh 1987).

For example, results from our pitfall data do not completely agree with preliminary results from >6,000 trap nights using live traps or from 20 time-constraint searches, both done at TR (Block, unpubl. data). In particular, we captured more *Perognathus californicus* and *Reithrodontomys megalotis* using live traps than we did using pitfall traps, but have captured no *Microtus*, *Sorex*, *Thomomys*, or *Scapanus* in live traps whereas we have caught them in the pitfalls.

Thus, researchers should compare and evaluate results from alternative methods to determine the most effective

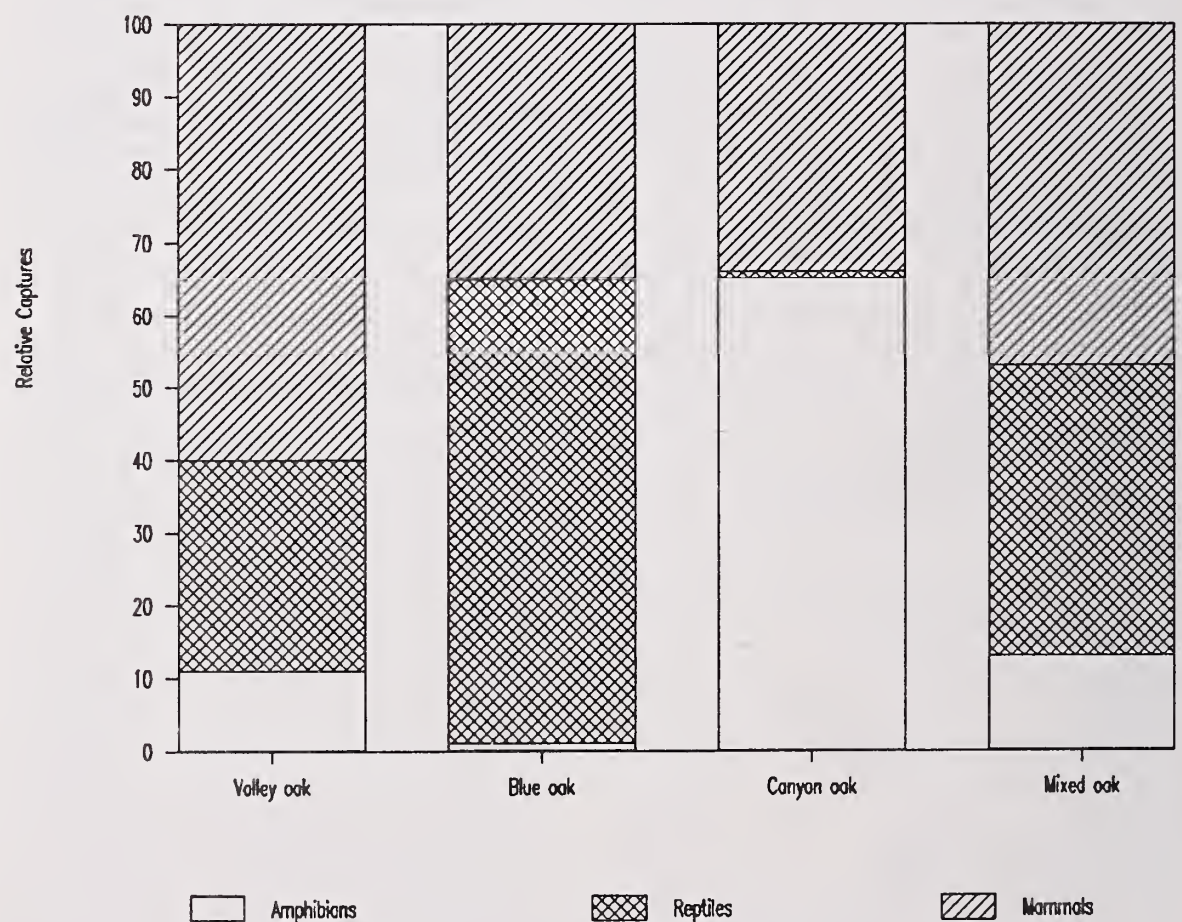


Figure 1.—Relative numbers of captures using pitfall traps within four oak woodland types at Tejon Ranch, Kern County, California from 5 December 1987 to 20 June 1988.

tive method or combination of methods to use for the species under study.

We evaluated our data in two different ways: comparisons of capture numbers and comparisons of trap success. Results from both analyses were generally consistent, although in some cases we found differences in comparisons of trap success, but failed to do so in comparisons of capture numbers. The discrepancies between these results may be attributable to both statistical and biological factors.

Statistical factors stem from the fact that continuous data were recorded for capture numbers whereas categorical data were recorded for trap success. Consequently, different statistical tests were required to analyze the different types of data. The

lack of concordance between results may be the result of different assumptions of the different tests and of different powers of the associated statistics.

For example, in comparisons of capture numbers, our use of all captures from a trap for a given species may have violated assumptions of independence of samples; assumptions underlying most parametric and nonparametric statistical tests (e.g., see Sokal and Rohlf 1969, Marascuilo and McSweeney 1977). Conversely, using presence-absence data as we did in analyses of trap success avoids the problem of dependency. A shortcoming of using only presence-absence data, however, is that information of the numbers and hence relative abundance of animals captured might be lost.

CONCLUSIONS

Using pitfall traps to sample amphibian, reptile, and small mammal populations, we found pronounced variation within and among study areas, and within and between years in capture rates of all taxa and of many of the species studies. Implications of these results apply both to the design of studies for these animals as well as for their management. First, we recognize biases by using only pitfall traps to sample populations of free-ranging vertebrates, and we suggest that researchers evaluate all possible methods to determine the best one or combination of methods for the study of a particular organism(s). Second, within-year variation in capture rates suggests that researchers should design a study to sample seasonal variations in activities and in habitat use. Similarly, spatial variation, both within and among stand types and among distinct geographic locations, should be studied to better identify distributional limits of the species studied and to determine how specific habitats contribute to the survival and reproduction of the species. From a management perspective, understanding temporal and spatial variability in habitat use is critical when trying to provide suitable conditions for the animal to survive and reproduce. All oak woodlands cannot be managed in the same way for all species. Each oak-woodland type contains a unique set of factors that predispose species to use the area for some aspect of their life histories. Management for a species should be based on information that considers the spatial and temporal variability in habitat use to provide for all life requisites.

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Table 2.—Capture numbers of amphibians, reptiles, and small mammals at three California oak woodlands: Tejon Ranch, Kern County; San Joaquin Experimental Range, Madera County; and Sierra Foothill Range Field Station, Yuba County, from mid-January through mid-March 1988.

Species	Tejon Ranch (n=8828) ¹	San Joaquin Exp. Range (n=8828)	Sierra Foothill Range Field Stn. (n=6912)
<i>Batrachoseps attenuatus</i> ²		8	1
<i>Batrachoseps nigriventris</i> ²	19		
<i>Ensatina eschscholtzii</i> ²	3		
<i>Taricha torosa</i>		1	
<i>Rana boylei</i>	1		
<i>Scaphiopus hammondi</i>		3	
<i>Sceloporus occidentalis</i> ²	20	31	96
<i>Eumeces gilberti</i> ²	9	46	
<i>Eumeces skiltonianus</i> ²			8
<i>Gerrhonotus multicarinatus</i>	1		1
<i>Peromyscus maniculatus</i>	6	7	3
<i>P. boylii</i>	13	6	5
<i>P. truei</i>	5	9	4
<i>Perognathus californicus</i>	1		
<i>P. inornatus</i>		1	
<i>Microtus californicus</i>	1		6
<i>Thomomys bottae</i>	1	4	1
<i>Scapanus latimanus</i>	1		
<i>Sorex ornatus</i>			3
Total captures	82	113	128
Species richness	13	10	9

¹Number of trap nights.

²Significant difference ($P < 0.10$) of captures among study areas.

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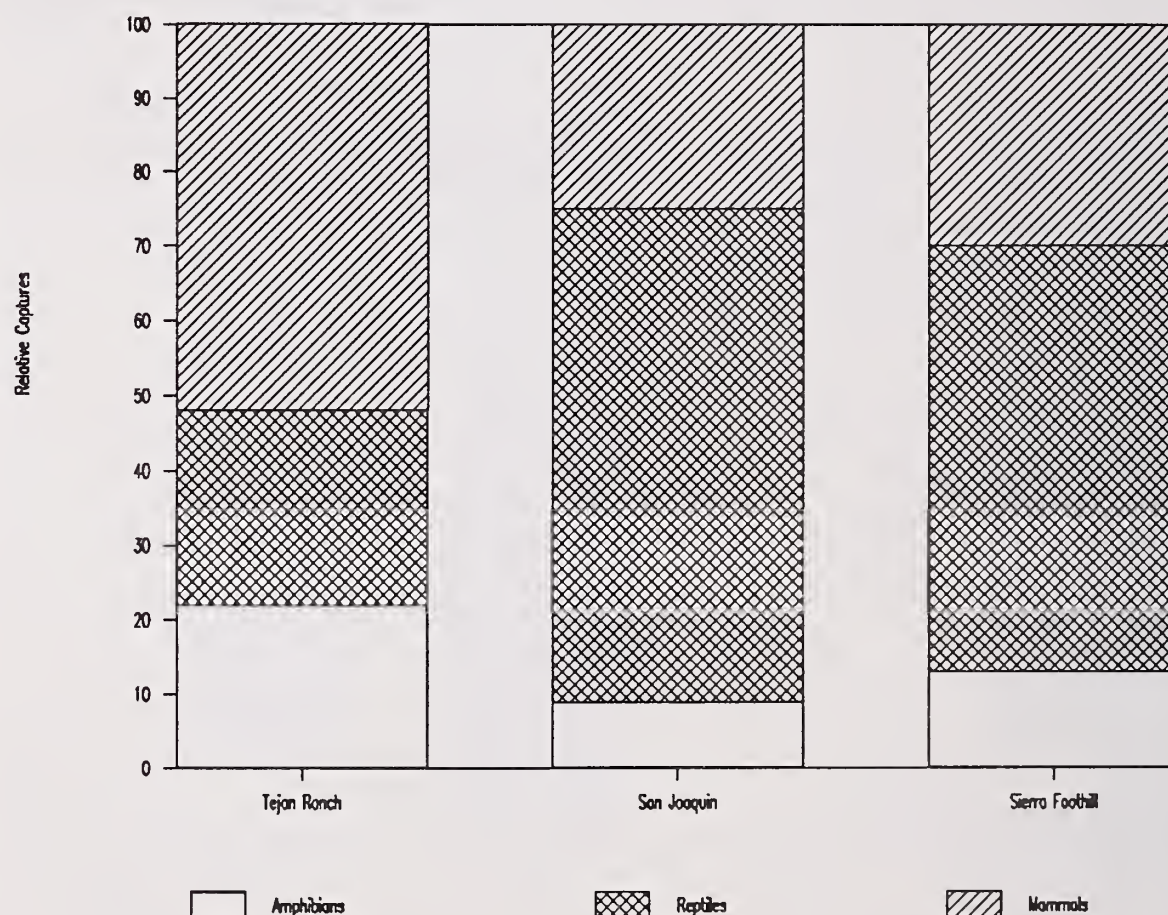
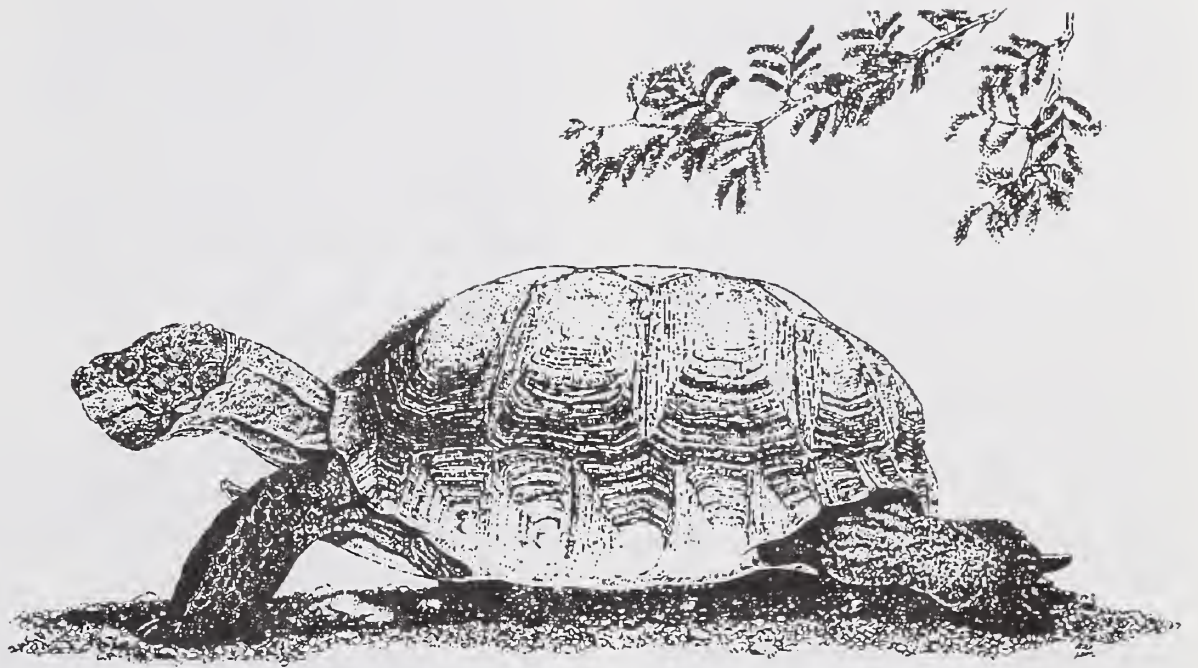


Figure 2.—Relative numbers of captures using pitfall traps within three oak woodland study areas in California: Tejon Ranch, Kern County, San Joaquin Experimental Range, Madera County; and Sierra Foothill Range Experimental Field Station, Yuba County. Trapping occurred from 5 December 1987 to 20 March 1988.

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The Importance of Biological Surveys in Managing Public Lands in the Western United States¹

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The equilibrium model of island biogeography (MacArthur and Wilson 1963, 1967) spawned a plethora of studies that examined ways in which various kinds of insular faunas behave (for mammals see Heaney and Patterson 1986). Some of the most interesting applications of the model have been to animals in islands of habitat, such as mountains in the Great Basin (Brown 1971, 1978). These studies revealed that such faunas often behave in contrast to the model, which predicts that the number of species on an island reflects an equilibrium between processes of origin, i.e., species emigrating to the island as a function of island size and distance from the mainland, and processes of extinction on the island. Such studies lend support to the contention that montane mammalian faunas in the Southwest are not in equilibrium (Brown 1986); rather, they are relicts derived by extinction

from a set of colonizing species that reached the mountains when life zones were lowered during the Pleistocene.

Newmark (1986a, 1986b, 1987) recently examined ways in which western North American national parks also behave, biologically, as islands. Newmark's (1986a, 1986b) analysis of data for 29 parks (data from only 24 were used in most analyses) in the United States and Canada showed that the number of mammalian species in these parks is declining.

Newmark (1986a, 1986b) predicted that western national parks, under a program of minimal management, could lose up to 100% of the extant species of lagomorphs, carnivores, and artiodactyls in the next 100 to 200 years. This loss of species would be dependent upon the original size of the park (larger areas have more species and larger populations that persist better through time), the degree of insularization of the parks (although most parks presently are not completely isolated, the more isolated they are, the less likely they will be colonized from outside), and intensity of management both within and outside park boundaries.

One of the mammalian faunas included by Newmark (1986a, 1986b) in his analysis was that of Dinosaur National Monument (DNM), located in northwestern Colorado and adjacent Utah, where few studies of mammals have been conducted. Gen-

Abstract.—Despite previous studies, incomplete knowledge of the mammalian fauna of many national parks hinders our ability to understand the consequences of either management actions or natural disasters to such preserves. Faunal losses have occurred and can be expected to continue (Newmark 1986a, 1986b). Our studies in and near Dinosaur National Monument, one of the parks studied by Newmark (1986a, 1986b), have added 11 species to the known fauna. Some species have increased with human impact; other species have either disappeared or are declining. Finally, many species, which are uncommon and poorly known, may have rather specific habitat needs.

eral information is available in only a few sources (Cary 1911, Warren 1942, Lechleitner 1969, Armstrong 1972), each of which treats all Coloradoan mammals. Detailed studies of this area are not common and may be difficult to obtain (Durrant 1963, Bogan et al. 1983). This paucity of knowledge is frustrating not only to mammalogists, but also to land managers seeking to protect the resources under their care. In the absence of reliable information, land stewards may end up managing for a relatively small portion of the total fauna, primarily those that are rare or endangered, highly visible or popular, pests, or those of importance to hunters and trappers.

Our studies in DNM and adjacent Browns Park National Wildlife Refuge, conducted since 1980, have provided new information on the mammals of northwestern Colorado. In addition, our data can provide a perspective on 1) the severity of the problem of faunal loss as shown by Newmark (1986a, 1986b) for one area (DNM); and 2) the continuing need for a better data base from which to manage parks and their fauna and flora. We summarize the gradual acquisition of knowledge about mammals in DNM, the contribution of recent detailed studies to the faunal data base, and how some species seem to be responding to human activity. Finally, we comment on some of Newmark's (1986a, 1986b) data and conclusions for DNM.

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Methods

Data were obtained from our studies conducted in northwestern Colorado since 1980. These studies, conducted in riparian and upland habitats in and near DNM, involved biological surveys for mammals and their sign. Mammals were observed, trapped and released, and collected. Specimens form a major part of our data base, confirming the actual presence of a species at a point in time.

Most habitats were sampled from one to three nights with 250 to 300 live or snap traps each night. Traps were set both in linear transects and opportunistically; mist nets and other methods were used for some species. Our study sites included campgrounds, subjectively categorized according to use by humans, as well as isolated areas rarely visited by humans. Although data from some

sites are directly comparable and statistically testable due to standardizing numbers of traps and techniques, our purpose here is to present an overview of the mammals at DNM using all available information.

Data on distribution and abundance of mammals in this part of Colorado came from four primary sources; these are Cary (1911), Warren (1942; a slightly revised version of Warren 1910), Lechleitner (1969), and Armstrong (1972). Studies of nearby areas were consulted (Kirkland 1981, Finley et al. 1984, Finley et al. 1976). Original surveys of DNM by Durrant (1963) and Bogan et al. (1983) were of value, as were observations and reports by knowledgeable park visitors and specimens in collections. Historic accounts (e.g., Wishart 1979) of fur trappers and explorers of the nineteenth century were reviewed for additional infor-

mation on the occurrence and disappearance of some game species undocumented by specimens.

Specimens of mammals from DNM are contained in the University of Utah Museum of Natural History (UU), the University of Colorado Museum (UCM), the Denver Museum of Natural History (DMNH), and the Biological Surveys Collection of the U. S. Fish and Wildlife Service in Washington, DC (USNM), and Fort Collins, CO (BS/FC). Original field notes, photographs, and catalogs form an important part of this data base and are available for inspection. Names of mammals follow Banks et al. (1987).

Results and Discussion

Historic Data Acquisition

The growth in knowledge of the mammals of DNM is shown in table 1. Data in Cary (1911), who worked just east of the present Monument and used both specimen data and his own and others' reports, suggest that about 42 species (65% of the species listed in appendix 1) occurred in or near DNM. Warren (1942), who did limited work in northwestern Colorado, provides information suggesting that perhaps 39 species occurred there. Lechleitner's (1969) general treatise on Coloradoan mammals, although not intended to provide detailed information on distribution, supports an expected fauna of about 50 species. Armstrong (1972), in the first comprehensive study of Coloradoan mammals, and building upon a sixty-year data base, relied on specimen data to confirm the presence or absence of mammals in a given area and recorded 47 species (72% of those currently known) for DNM or nearby areas. Although some of these references perhaps should not be used to infer the specific occurrence of species in a given area, we think they are so used by land managers and others.

Table 1.—Numbers of species of mammals at Dinosaur National Monument per order as given in various reports on Colorado mammals (see text). Percentages in parentheses are the proportion of the total mammal fauna that a given order represents.

ORDER	REFERENCE					
	Cary 1911	Warren 1942	Lechleitner 1969	Armstrong 1972	Newmark 1986a	This paper 1988
INSECTIVORA (1.5%)	0	0	?	0	0	1
CHIROPTERA (21.5%)	4	3	7	8	13	14
LAGOMORPHA (6.1%)	3	3	3	3	4	4
RODENTIA (38.5%)	18	18	21	20	19	25
(SCIURIDAE)	6	7	7	8	6	9)
(GEOMYIDAE)	1	1	1	1	1	1)
(HETEROMYIDAE)	1	2	2	2	2	3)
(CRICETIDAE)	8	6	9	8	8	10)
(OTHER)	2	2	2	1	2	2)
CARNIVORA (24.6%)	13	11	15	12	19	16
ARTIODACTYLA (7.6%)	4	4	4	4	6	5
TOTALS	42	39	50	47	62*	65
(%)	65	60	77	72	95	100

*Includes nine species that are not known from DNM.

During the period covered by these references little actual work on the mammals of DNM was conducted. Exceptions were the work of Hayward et al. (1958), Durrant and Dean (1959, 1960), and Durrant (1963) who chronicled the only extant baseline data for many riparian areas along the Colorado River and its major tributaries (Green, Yampa) prior to the impoundments at Flaming Gorge and Glen Canyon.

Durrant (1963) surveyed for mammals in DNM and reported 24 species collected or observed, about 37% of the known fauna. Two later surveys for mammals and other vertebrates in the Monument produced 29 (Bogan et al. 1983) and 27 (Bogan unpubl. data) species, 45% and 42% of the presently known fauna. Many of the same species were obtained on both trips.

Contributions of Recent Surveys

The known fauna of DNM includes 65 species (appendix 1) based on specimens and reliable sight records. Three species (*Canis lupus*, *Ursus arctos*, and *Bison bison*) are now extirpated; we have omitted one species of dubious occurrence (*Mustela nigripes*). The percentage of mammalian species at DNM by order is Insectivora, 1.5%; Chiroptera, 21.5%; Lagomorpha, 6.1%; Rodentia, 38.5%; Carnivora, 24.6%; and Artiodactyla, 7.7%. Horses (*Equus caballus*) and house mice (*Mus musculus*) occur at DNM; we have excluded these introduced species from our list.

What result have enhanced levels of faunal surveys had on the known fauna of DNM? Our work has added 11 species to the known fauna. These include two state records [*Perognathus parvus* and *Euderma maculatum* (Finley and Creasey 1982) from Browns Park National Wildlife Refuge, about 8 mi from DNM]; one county record (*Lepus californicus*) from DNM; seven Monument records in 1982 (*Myotis californicus*, *M.*

thysanodes, *Lasionycteris noctivagans*, *Pipistrellus hesperus*, *Perognathus parvus*, *Microtus longicaudus*, and *M. montanus*); and three records for the Monument in 1987 (*Sorex monticolus*, *Euderma maculatum*, and *Lemmys curtatus*).

These 11 species represent an increase of 20.3% over the number previously known from DNM. Much of this increase (five species) has come by acquiring a better understanding of the bats. This has been possible because of better techniques of surveying for bats, an improved understanding of continental and regional distributions of bats, and an enhanced effort in surveying for bats at DNM. Additional knowledge of some other groups has come more slowly, primarily because we are approaching the asymptote with respect to species occurring in DNM. The number of cricetid rodents known or suspected to occur has increased from eight to ten in 75 years; that for sciurids has increased from six to nine. Armstrong (1972) reported 20 rodents known from DNM; our records reveal a rodent fauna of 25 species. For bats the figures are 8 in 1972 and 14 in 1987, an increase of 75%.

The extent to which surveys reveal previously unknown faunal components is both fortuitous and regulated by biological phenomena. The capture of the first records of shrews and spotted bats from DNM is partly luck, by being in the right place at the right time. Yet this ability to "test" distributions of mammals by examining (trapping) suitable habitats requires training, skill, and knowledge. In addition, the ability to find rare animals often requires removing the more abundant and common species.

For example, of the 1,469 specimens of small mammals that we have captured at DNM, 52.6% have been *Peromyscus maniculatus*. We have taken 1,049 *Peromyscus* (71.4% of the total trapped) as follows: *P. maniculatus*, 772; *P. truei*, 175; *P. crinitus*, 102. There may be many reasons

why so many *Peromyscus* are taken; our techniques may be biased in favor of them, they are easily trapped, etc. Still, they are abundant relative to other species of mammals on the Monument.

We have no exact density figures for *P. maniculatus* in DNM but extrapolations are possible. The area of DNM is 827 km² or 82,700 ha; an average density for *P. maniculatus* might be 20/ha (French et al. 1975), or 1,654,000 deer mice. We suspect that the densities at DNM are higher, at least seasonally. A higher density of 50/ha (French et al. 1975) would yield 4,135,000 deer mice. If the average deer mouse weighs 20 g (a low estimate), then the deer mouse biomass at DNM is 33,080 kg to 82,700 kg; the equivalent of 144 to 360 adult elk (*Cervus elaphus*) weighing 230 kg each. The current resident elk population of DNM is 150 to 200; up to 600 may be resident seasonally.

This abundance has several implications. One is that the common species can fill the traps, reducing the possibility of captures of other species, and thus biasing the catch. More interestingly, an accurate understanding that there are a few abundant species and many uncommon ones can provide information of value in assessing impacts of human activities and management of the park, e.g., what species appear to be increasing, those that are decreasing or extirpated, those that are adjusting their ranges, and those for which we have insufficient information. Examples for these categories are discussed below.

Management Implications

Species Increasing in Abundance.—*Peromyscus maniculatus* has been suggested (Armstrong 1977, 1979) as one species that increases in areas disturbed by humans. It is a widespread and adaptable species; whether it has actually increased in some situations, such as in campgrounds, may be de-

batable. Armstrong (in litt.) has noted that deer mice are weed species and that rather than representing a moral failure, they represent a successful evolutionary strategy. *P. maniculatus* apparently always has been common in this part of Colorado; Cary (1911:103) stated that this species was "exceedingly numerous despite coyotes, hawks, and owls...in western Routt [now Moffat] and Rio Blanco Counties in 1906..." He reports (1911:103) that in one case their "excessive numbers all but prevented my securing topotypes" of another species, and that near Lodore they were everywhere a "great nuisance."

Our data from DNM reveal that the canyon mouse (*P. crinitus*) is a specialist of rocky canyon areas. It does penetrate to the upper reaches of some canyons but rarely does it spread much further. The pinon mouse (*P. truei*) is a specialist of pinon-juniper forests and occasionally becomes moderately abundant. Conversely, *P. maniculatus* is common in sagebrush (*Artemisia* sp.) flats, a common upland habitat at DNM. A comparison of relative abundance of this species in subjectively categorized "natural" and "campground" situations reveals an average of 22.4 animals/locality ($n = 16$) in areas where camping is of low intensity or absent, versus an average of 29.6 deer mice/locality in 14 heavily-used areas. Although these numbers cannot be tested for significance, due to non-uniform trapping procedures, there is a difference in relative abundance of *P. maniculatus*.

Another species that appears to show a "campground" effect is the golden-mantled ground squirrel (*Spermophilus lateralis*). We have taken this species in many areas and it is widespread. Cary (1911:84) reported that this species was "said to be abundant" near Lily (just outside the present Monument), and 7 mi N of Lily they were reported to be "tolerably common," but Cary saw none there the previous year. They are so

common in campgrounds of the Monument now that they are a nuisance, albeit an attractive one. They are fed by visitors and thus are encouraged to remain near the campgrounds. Our data from areas subjectively categorized in terms of human use reveals an average of 7.1 ground squirrels from eight areas heavily used by humans versus 1.2 animals/locality in six little-used areas. In areas where golden-mantled ground squirrels are very common we routinely close our traps during the day to prevent being overrun with these animals.

Species Declining or Disappearing.—Those elements of a fauna that disappear over time are clearly of concern, and may provide clues to habitat changes or other factors leading to faunistic changes. At least three mammalian species are now extirpated from DNM, and likely from Colorado. These are the gray wolf (*Canis lupus*), the grizzly bear (*Ursus arctos*), and the bison (*Bison bison*). Armstrong (1972) cites a specimen of *C. lupus* from Douglas Spring, near the present-day Monument. That gray wolves were common is shown by the fact that about 50 were killed by hired trappers in Brown's Park in the winter of 1906-07 (Cary 1911). *C. lupus* was not included in the DNM fauna by Newmark (1986a).

No specimen of *U. arctos* from or near the Monument is known to us, but there are reports of sightings in the 1800s. About 60 fur trappers and 800 Indians wintered in Brown's Park in 1839-40, during which time they killed six grizzlies and 100 bison for meat (Dunham and Dunham 1977). Fresh tracks of grizzlies were seen in 1871 by members of the second Powell expedition in Lodore Canyon, a few miles above Echo Park (Dellenbaugh 1926); and in 1891 Ann Willis was rescued from a female grizzly with two cubs in Zenobia Basin (Murie and Penfold 1983).

Remains of *B. bison* were excavated from Hell's Midden, an occu-

pation site of the Fremont Culture in Castle Park (Lister 1983). In addition, Walker (1983) reports the recovery of remains of bison, as well as black bear (*U. americanus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), wapiti (*Cervus elaphus*), and bighorn sheep (*Ovis canadensis*), from Fort Davy Crockett in Brown's Park. These remains date from between 1836 and 1842. Ashley saw several bison in Island Park in 1825 (Murie and Penfold 1983).

The dates of disappearance of these species are speculative. *B. bison*, which wintered in Brown's Park, was already in decline west of the Continental Divide in the late 1830s, as observed by concerned fur trappers (Wishart 1979). According to Wishart (1979), the Rocky Mountain trapping system in Wyoming and Colorado decayed not only because its main fur-bearer, the beaver, was depleted but also because the main source of provisionment, the mountain bison, was destroyed. Termination of the fur trade in 1840 allowed mountain bison to persist for several decades. The last bison killed in northwestern Colorado was at Cedar Springs west of Craig in 1884 (Armstrong 1972).

C. lupus seems to have disappeared by 1935-40 (Young 1944, Lechleitner 1969). The last report of *U. arctos* in northern Colorado was in 1920 in the Medicine Bow Range (Armstrong 1972). Both species were victims of increasing human encroachment and active predator control campaigns.

We have chosen to exclude the black-footed ferret, *Mustela nigripes*, from the known fauna of the Monument, for lack of specimens and sightings, although it was included by Newmark. Generally, the ferret appears to have been a victim of the active poisoning of its principal prey, prairie dogs (*Cynomys* spp.) in addition to other factors (Clark 1986, Flath and Clark 1986).

Newmark (1986a) stated that wapiti (*Cervus elaphus*) should be added to the list of mammals extir-

pated from DNM. Wapiti did occur in the Monument in the early nineteenth century and are there today, but their origin is questionable.

The present animals may be descended from remnant populations from elsewhere in parts of northern Colorado or Utah, or from later introduced wapiti from Wyoming. We suspect they may be of mixed descent.

Ovis canadensis occurring on the Monument today may likewise be of mixed descent. As noted by Pillmore (unpubl. ms.) bighorn were common and highly desired for food by trappers and explorers in northwestern Colorado in the first half of the 1800s, but were greatly reduced by the 1880s, when they were protected by the first game laws. Thereafter the herds slowly increased until heavy die-offs were caused by diseases from domestic sheep. Such losses occurred in Lodore Canyon between 1936 and 1945. By 1947 the superintendent at DNM was ready to "write them off." In 1954 the Colorado Game and Fish Department made two transplants in Lily Park and Zenobia Peak, and numbers since have increased in the Monument (Murie and Penfold 1983).

At least two species may be adjusting their ranges relative to each other in reciprocal fashion. We are aware of no reports of *Lepus californicus* in Moffat County prior to about 1980, although both specimens and sightings of *L. townsendii* exist. In 1972 in western Colorado, the northernmost locality for *L. californicus* was Mesa County (Armstrong 1972). In the summer of 1987, we captured both species, in close proximity, in DNM. Based on the pattern of replacement seen elsewhere, including the eastern plains of Colorado (Armstrong 1972), it is possible that the range of *L. townsendii* is contracting to the north and that of *L. californicus* is expanding to the north. This replacement is commonly tied to land use practices, especially breaking the ground for cultivation, or over-

grazing, which may lead to increased amounts of *Opuntia* (Armstrong 1972). Whether *L. californicus* is actually replacing *L. townsendii* at DNM is debatable; what is not arguable is that *L. californicus* is extending its range northward in western Colorado.

Species for Which Information is Inadequate.—There are many species for which scant information exists. These species include most of the insectivores, bats, and rodents, together composing 61.5% of the mammalian fauna of the Monument. Of the 40 species in this category, almost one-third were unknown at DNM just 15 years ago. Much of this increase comes from a better understanding of the bats, but knowledge of their presence does not tell us if there are important hibernacula for bats on DNM, what proportion of the bats may be migratory, or how best to manage for this significant component (22%) of the fauna. Similar comments can be made for most of the other small mammals, although few are as vulnerable to mismanagement and destruction as are bats (Hill and Smith 1984).

Cottontails (*Sylvilagus* spp.) are commonly seen, even abundant at times, but it is difficult to identify animals with certainty as the two species (*S. audubonii* and *S. nuttallii*) occurring at DNM are externally similar. The two species overlap in northwestern Colorado between approximately 6500 ft and 7000 ft and specimens of both were collected by Warren at Douglas Spring. The nature of interactions between the two species of cottontail at DNM is unknown and studies based on specimens are needed.

The raccoon was likely absent from the park and probably the entire upper Colorado River basin prior to the 1950s (Durrant 1952, Long 1965). Specimens (BS/FC) indicate that they moved into the upper Green River and Brown's Park in the 1960s and 1970s, probably from eastern Wyoming.

Newmark's Analysis Applied to Dinosaur National Monument

Newmark's (1986a) analysis is important because it stimulates us to consider a problem and assess its magnitude, and also because he suggests some solutions. He predicts a depressing picture for some species in national parks and there is clear cause for concern. Still, it is useful to put his analysis in perspective. Newmark (1986a) lists 62 species of mammals as occurring in DNM, including *E. caballus* but not *M. musculus*. He (1986a:21) confined his analysis to only three orders, lagomorphs, carnivores, and artiodactyls "because these orders had the most complete park sighting records. Species of these orders tend to be more frequently reported because of their relatively large body size, non-fossorial nature, and popularity." He also used park sighting records as well as continental (Hall 1981), statewide (Armstrong 1972), and local (Anderson 1961) reports.

Those orders used by Newmark (1986a) in his analysis include 39% of the known mammalian species at DNM. The most diverse order (Rodentia) and the third most diverse order (Chiroptera) at DNM are excluded. Furthermore, the 22 species he does consider include the only faunal losses (5) he believes occurred in DNM. We believe that only three species are extirpated from DNM, and further suspect that most of the extinctions occurred prior to major expansion of the Monument's boundaries (1938).

However, the best management decisions will be derived from the most accurate data, and we should try to obtain such data. We also believe that a holistic approach to animal management on public lands is needed. This means including small and secretive species in our plans, as well as the large "glamorous" ones. Newmark recognizes this in his recommendations; he notes the need to develop a more extensive monitoring

program for vertebrate populations, including key species of every order.

An examination of Newmark's (1986a) data reveals that nine of the 62 species he lists for DNM do not occur there: *Plecotus rafinesquii* (an eastern bat perhaps listed due to a misunderstanding of its taxonomy), *Tadarida brasiliensis* (accidental at best, no records for northern Colorado), *Lepus americanus* (perhaps confused by an observer with *L. townsendii* in all-white winter pelage), *Glaucomys sabrinus* (may possibly occur in higher areas of Douglas Mountain at DNM but presently unknown), *Peromyscus boylii* (perhaps mistaken by an observer for the large-eared *P. truei*), *Vulpes velox* (no specimens north of Mesa County), *Gulo gulo* (there is a specimen from near the Utah-Colorado stateline, outside the Monument), *Mustela erminea*, and *Alces alces* (accidental stragglers only).

Why some of these species were included by Newmark is unknown, but in some cases it may have been because they were listed in park records, compiled from observations by visitors and staff. We reexamined the records at DNM and also found records (mostly sightings) of *Sorex cinereus*, *Tamias umbrinus*, *Perognathus flavescens*, *Ammospermophilus leucurus*, *Neotoma lepida* (perhaps juveniles of *N. cinerea*), and *Zapus hudsonius*. We know of no specimens to substantiate these records and do not include them in the fauna of the Monument.

These errors are not necessarily Newmark's, although he may have been uncritical in some instances, but likely stem from several sources.

Among these are inadequate or lacking baseline surveys, inaccurate record-keeping by park staff, misunderstandings of current nomenclature by observers or recorders, unreliable observations, and human error. Nonetheless, these errors cloud our understanding of mammals at DNM and the management problems they present. Additionally, although all data and results age with time, New-

mark did not have the most current information in many cases and thus was unaware of recent records of mammals from DNM.

Conclusion

Lists of species from a given area are subject to interpretation. We have taken a conservative approach relying on specimens (and giving reasons for inclusions and exclusions where appropriate) and have added significantly to the known mammalian fauna of DNM. Such lists are not trivial exercises because they are the raw materials for making land management decisions. Incorrect or missing data will diminish our ability to manage these lands and their faunas. We believe that biological surveys, resulting in verified records (preferably specimens, but sometimes other data), are the only reliable means to determine the presence of a species and to monitor population trends over time. We agree with Newmark (1986a) that such surveys need to be undertaken immediately, because the information is needed now; and where surveys have been initiated they should be continued on a regular basis. Monitoring of animal populations and the incorporation of accurate data into rational management plans is the only way to ensure that our public lands continue to support a diverse fauna that is as complete as possible.

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Appendix 1

List of mammalian species from Dinosaur National Monument. Species are represented by specimens in collections unless otherwise noted in parentheses. Those specimens not in the U. S. Fish and Wildlife Service's Biological Surveys Collections in Fort Collins (BS/FC), or known only from near the Monument, are so noted in parentheses. See text for species excluded from this list. Additional information on specimens or sight records is available from the authors.

Sorex monticolus (Montane shrew)
Myotis californicus (California myotis)
Myotis ciliolabrum (Western small-footed myotis)
Myotis evotis (Long-eared myotis)
Myotis lucifugus (Little brown bat; 5 mi SE Elk Springs, UCM)
Myotis thysanodes (Fringed myotis)
Myotis volans (Long-legged myotis)
Myotis yumanensis (Yuma myotis)
Lasiurus cinereus (Hoary bat)
Lasionycteris noctivagans (Silver-haired bat)
Pipistrellus hesperus (Western pipistrelle)
Eptesicus fuscus (Big brown bat)
Euderma maculatum (Spotted bat)
Plecotus townsendii (Townsend's big-eared bat)
Antrozous pallidus (Pallid bat)

Sylvilagus audubonii (Desert cottontail)
Sylvilagus nuttallii (Nuttall's cottontail)
Lepus californicus (Black-tailed jackrabbit)
Lepus townsendii (White-tailed jackrabbit)
Tamias dorsalis (Cliff chipmunk)
Tamias minimus (Least chipmunk)
Tamias quadrivittatus (Colorado chipmunk)
Marmota flaviventris (Yellow-bellied marmot; Castle Park, UCM)
Spermophilus lateralis (Golden-mantled ground squirrel)
Spermophilus elegans (Wyoming ground squirrel; Two Bar Spring, DMNH)
Spermophilus tridecemlineatus (Thirteen-lined ground squirrel)
Spermophilus variegatus (Rock squirrel)
Cynomys leucurus (White-tailed prairie dog)
Thomomys talpoides (Northern pocket gopher; Pot Creek, DMNH)
Perognathus fasciatus (Olive-backed pocket mouse)
Perognathus parvus (Great Basin pocket mouse)
Dipodomys ordii (Ord's kangaroo rat)
Castor canadensis (Beaver)
Reithrodontomys megalotis (Western harvest mouse)
Peromyscus crinitus (Canyon mouse)
Peromyscus maniculatus (Deer mouse)
Peromyscus truei (Pinon mouse)
Onychomys leucogaster (Northern grasshopper mouse)
Neotoma cinerea (Bushy-tailed woodrat)
Microtus longicaudus (Long-tailed vole)
Microtus montanus (Montane vole)
Lemmiscus curtatus (Sagebrush vole)
Ondatra zibethicus (Muskrat; Castle Park, UCM)
Erethizon dorsatum (Porcupine; Pot Creek near Pat's Hole, DMNH)
Canis latrans (Coyote)
Canis lupus (Gray wolf, +; Douglas Spring, UCM)
Vulpes vulpes (Red fox; ca. Zenobia Peak, Cary 1911)

Urocyon cinereoargenteus (Gray fox; Castle Park, UCM)
Ursus americanus (Black bear)
Ursus arctos (Grizzly bear, +)
Bassariscus astutus (Ringtail; Castle Park, UCM)
Procyon lotor (Raccoon)
Mustela frenata (Long-tailed weasel; Castle Park, UCM)
Mustela vison (Mink; sightings in Lodore Canyon)
Spilogale gracilis (Western spotted skunk; Irish Canyon, ca. Lodore)
Mephitis mephitis (Striped skunk)
Taxidea taxus (Badger; Two Bar Spring, DMNH)
Lutra canadensis (River otter; Yampa Canyon, Warren 1942)
Felis concolor (Mountain lion; Greystone, UCM)
Felis rufus (Bobcat)
Cervus elaphus (Wapiti)
Odocoileus hemionus (Mule deer; Pot Creek, USNM)
Antilocapra americana (Pronghorn)
Bison bison (Bison, +)
Ovis canadensis (Bighorn sheep)

(+ = species is extirpated from the Monument)

Sampling Problems in Estimating Small Mammal Population Size¹

George E. Menkens, Jr.² and Stanley H. Anderson³

Abstract.—Estimates of population size are influenced by four sources of error: measurement, sampling, missing data, and gross errors. Measurement error can be reduced by using the correct estimator, reducing variation in capture probabilities, and by increasing sample size and trap period length. Sampling error can be decreased by increasing the number of grids trapped.

Species conservation and management or analysis of environmental impacts require accurate estimates of population size. Because censusing entire populations is difficult, if not impossible, a sampling program is generally employed to estimate animal abundance. In small mammal studies, sampling is frequently performed using live traps placed in grids. Numerous approaches have been used to estimate animal abundance on trapping grids (e.g., catch-per-unit effort, removal methods) but capture-mark-recapture techniques are the most commonly used (Seber 1986).

Four sources of error may influence an estimator's bias and precision (Cochran 1977, McDonald 1981). Two, missing data and gross errors (e.g., misreading tag numbers) are "human" errors and can be avoided by using careful field and laboratory techniques. The remaining sources,

measurement and sampling error, may, in many cases greatly affect an estimate (McDonald 1981). Measurement error is the error resulting from the use of imprecise or biased (or a combination of these) data collection methods (McDonald 1981). In mark-recapture studies, measurement error influences the bias and precision of an estimate for any single grid. Sampling variance is considered to be a measurement error in mark-recapture studies (White et al. 1982). Sampling error is error introduced by natural variation between sampling units, i.e., trap grids.

Potentially large sources of measurement error in mark-recapture studies may result from capture probability variation and model selection. All mark-recapture estimators make specific assumptions about capture probability variation within and among animals and trapping days. Three factors influencing individual capture probability variation have received attention (Burnham and Overton 1969, Otis et al. 1978, Pollock 1981, Seber 1982) and are time, behavior, and individual heterogeneity. Models assuming time variation allow all animals to have the same capture probability on a given day, but this probability may change between days. Models allowing behavioral responses to trapping assume all animals initially possess identical capture probabilities, but these probabilities may change upon first capture. Capture probabilities

may increase (animals become trap happy) or decrease (animals become trap shy) after initial capture. Models assuming that individual heterogeneity is present allow each animal to have a unique capture probability that does not change over time. Combinations of these factors may also occur. For example, an animal's capture probability may be influenced by both time and behavioral effects.

Model selection is another source of measurement error. Selection of an inappropriate or incorrect model for data analysis results in estimates with unknown degrees of bias and unacceptably large or unrealistically small standard errors (Otis et al. 1978, White et al. 1982). CAPTURE (Otis et al. 1978) is a widely used computer program for estimating population size using mark-recapture data that also provides an objective method for selecting the correct model when any of the above sources of capture probability variation are present.

In this paper, we investigate the effects that variation in capture probabilities due to time, behavior, and individual heterogeneity have on estimates of animal abundance and model selection. We also discuss improvement of an estimate using data pooling. We use these results to show how reducing trap period length influences estimator bias, standard error, and confidence interval coverage rate, and discuss how this may help reduce the number of

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grids required to detect a given difference between yearly estimates of population sizes.

Material and Methods

To investigate effects of both capture probability variation and trap period reduction, we used program CAPTURE (Otis et al. 1978) to randomly generate and analyze data sets with known population characteristics (see Menkens 1987 for details). CAPTURE contains eight models, five with estimators, for estimating population size for closed populations when capture probabilities do not vary (model M(o)), or when they vary with time (model M(t)), behav-

ioral response (model M(b)), individual heterogeneity (model M(h)) or a combination of the behavioral and individual heterogeneity models (model M(bh)). Using CAPTURE, we specified the number of trapping periods, population size, and capture probabilities, and patterns of variation. CAPTURE was then used to analyze each data set.

We analyzed the same data sets using Chapman's unbiased version of the Lincoln-Petersen estimator and its variance estimator (Seber 1982). Because the Lincoln-Petersen estimator uses data from only two periods, each data set was split prior to estimation. Thus in a 5 day trapping study, the first 3 days constituted the marking period, and the second 2

days was the recapture period. In studies 10 days long, the first 5 days were the marking period, the second 5 days the recapture period.

Data were generated for a wide range of conditions. We used trap periods of 5 and 10 days, population sizes of 50 and 100 and a wide variety of capture probability patterns (table 1). One thousand data sets were generated for each combination of these conditions. In this paper, we only generated data meeting the assumptions of one of the five models with estimators in CAPTURE. For each data set, CAPTURE was forced to perform the analysis using the correct model. For example, if data were generated under the assumption of time variation, CAPTURE was forced to use model M(t) for the analysis. Simulations were also performed using the same, and additional, capture probabilities (table 1), with CAPTURE being allowed to select an estimator using its model selection procedure.

Results

Performance of both the Lincoln-Petersen estimator and CAPTURE is dependent upon the size and magnitude of the variation in capture probabilities (table 2). Estimators have lower degrees of bias, smaller standard errors, and higher confidence interval coverage rates when capture probabilities are high and their variation is low (tables 1 and 2) over all population sizes. When capture probability variation is constant, the estimator's bias tends to decrease and confidence interval coverage rates increase with increasing population size (table 2). Although this pattern is evident for standard errors, patterns of change with increasing sample size are not as clear (table 2).

In general, the estimator's bias decreases and confidence interval coverage rates increase as trapping period length increases (table 2). This

Table 1.—Capture probability patterns used in simulations (from Menkens 1987 and Menkens and Anderson in press). Good capture probabilities are defined as being large (generally ≥ 0.30) with little difference (about 0.15) between the highest and lowest capture probability. Poor capture probabilities are defined as being low with large differences between the highest and lowest capture probability. "Model" refers to the CAPTURE model under which the data were generated. See the text for description of the model abbreviations. p = capture probability, c = recapture probability (trap shyness = $p(0.50)$, trap happiness = $p(1.50)$), all simulations were run for 5 and 10 day capture periods (t).

Model	Poor	Good
M(o)	$p = .1$	$p = .5$
M(h)	$p = 0.05, 0.10, 0.25^1$	$p = 0.40, 0.50, 0.60^1$
M(b)	$p = 0.10, c = 0.50$	$p = 0.50, c = 1.50$
M(bh)	$p = 0.05, 0.20, 0.40$ $c = 0.50$	$p = 0.20, 0.30, 0.40$ $c = 1.50$
M(t)	$p = 0.05, 0.20, 0.40$ $c = 0.50$ or 1.50^2	$p = 0.20, 0.15, 0.25$ $c = 0.50$ or 1.50^2
	$p = 0.10, 0.15, 0.05,$ $0.15, 0.10$ $t = 5$	$p = 0.50, 0.55, 0.40,$ $0.55, 0.50$ $t = 5$
	$p = 0.10, 0.10, 0.15,$ $0.15, 0.05, 0.05,$ $0.15, 0.15, 0.10,$ 0.10 $t = 10$	$p = 0.50, 0.50, 0.55,$ $0.55, 0.40, 0.40,$ $0.55, 0.55, 0.50,$ 0.50 $t = 10$

¹Three groups of animals were assumed to be present in the population, the first group was associated with the first capture probability, the second group with the second capture probability, the third group with the third capture probability. For $N = 50$, animals 1-20 were in group 1, 21-40 in group 2, 41-50 were in group 3. For $N = 100$, animals 1-40 were in group 1, 41-80 were in group 2, 81-100 were in group 3.

²When a heterogeneous recapture probability was assumed, half of the animals became trap shy, half became trap happy.

pattern is not as obvious for standard errors, although they do tend to improve with increasing trap period length (table 2). In most cases the magnitude of change in bias is smaller for good capture probabilities than for poor capture probabilities when the trapping period increases (table 2). Although estimated standard errors tend to decrease with lengthening trap periods (more so with good capture probabilities), the magnitude of this change is generally smaller than is change in bias (table 2). As with bias and standard error, confidence interval coverage rates improve as trapping period increases; the magnitude of change tends to be larger when capture probabilities are poor (table 2).

Except when data were generated under model M(o), CAPTURE selected the correct model less than 11% of the time (table 3). The Lincoln-Petersen estimator failed to provide an estimate at most 7% of the time (table 3).

Discussion

In small mammal studies, measurement errors can significantly influence an estimator's bias and precision. This study shows the importance of both reducing capture probability variation and increasing the size of those probabilities on measurement error. Decreasing capture probability variation reduces the estimate's bias and coefficient of variation, and increases its confidence interval coverage rate. This result has also been stressed by Burnham and Overton (1969), Menkens (1987), Menkens and Anderson (in press), Otis et al. (1978), and White et al. (1982). Of particular significance is the need to reduce variation due to behavioral responses (i.e., trap-happiness and shyness) and individual heterogeneity, especially when these factors act in concert (Menkens and Anderson in press, Otis et al. 1978, White et al.

Table 2.—Simulation results for N = 50 and 100 when CAPTURE was forced to use the correct estimator. CAPTURE refers to the appropriate CAPTURE model for analysis, L-P = Lincoln-Petersen estimate, Model is the model under which the data were generated by CAPTURE, P = poor capture probabilities, G = good capture probabilities (see table 1 for definitions), t = length of trapping period (in days), PRB = percent relative bias, SE = empirical standard error, CIC = confidence interval coverage rate.

Model	L-P				CAPTURE			
	50		100		50		100	
	P	G	P	G	P	G	P	G
M(o)								
t = 5								
PRB	-52.3	0.02	-34.9	-0.5	-9.0	1.4	17.3	-0.2
SE	0.5	0.2	0.9	0.3	1.0	0.2	2.3	0.3
CIC	27.6	87.0	57.1	91.2	80.7	90.7	87.5	92.1
t = 10								
PRB	-11.5	0.0	-2.5	0.0	18.3	-0.10	7.1	-0.50
SE	0.6	0.1	1.1	0.1	1.1	0.1	1.2	0.1
CIC	73.8	92.3	83.8	93.4	89.1	92.1	91.6	93.2
M(h)								
t = 5								
PRB	-55.4	-1.2	-40.9	1.6	-49.4	12.8	-43.0	16.5
SE	1.1	0.2	1.6	0.3	0.3	0.3	0.4	0.5
CIC	16.2	86.4	40.1	89.0	22.8	81.1	6.0	67.1
t = 10								
PRB	-28.2	-1.0	-24.9	-0.7	-16.1	7.2	-10.0	9.5
SE	0.6	0.1	1.0	0.1	0.5	0.2	0.8	0.2
CIC	48.0	87.9	52.4	91.4	52.8	92.3	59.9	63.2
M(b)								
t = 5								
PRB	-52.0	-12.2	-30.5	-12.1	-70.0	2.2	-59.1	3.2
SE	1.6	0.2	1.9	0.4	0.3	0.5	0.7	0.9
CIC	9.4	52.4	34.1	40.0	13.3	81.4	36.4	87.3
t = 10								
PRB	6.2	-4.0	43.7	-3.7	-33.3	-1.4	-12.3	-0.6
SE	0.7	0.1	2.3	0.1	0.6	0.1	1.7	0.1
CIC	66.6	54.3	91.3	43.6	49.7	82.4	64.8	89.9
M(bh) (set 1)								
t = 5								
PRB	-23.5	26.0	-23.1	45.8	-17.8	-17.8	-1.5	-1.5
SE	0.5	0.9	0.8	2.2	0.6	0.6	1.7	1.7
CIC	49.5	88.0	41.3	99.1	60.7	60.7	70.9	70.9
t = 10								
PRB	-0.4	-13.8	-13.7	27.9	-28.8	-4.1	-24.6	-3.5
SE	0.5	0.3	0.5	1.1	0.4	0.4	0.8	0.6
CIC	83.4	43.1	27.5	92.5	40.5	69.6	43.2	75.2
(set 2)								
t = 5								
PRB	-32.5	-17.8	-31.3	-3.6	-31.3	-40.6	-18.8	-22.1
SE	0.6	0.6	1.1	1.1	0.4	0.4	1.2	1.2
CIC	33.6	64.8	24.4	82.4	46.2	47.6	57.2	64.9
t = 10								
PRB	-20.5	0.2	-20.2	-0.2	-28.8	-4.9	-24.6	1.7
SE	0.4	0.4	0.7	0.5	0.4	0.6	0.8	1.4
CIC	32.1	86.7	17.2	91.2	40.5	67.7	43.2	73.5
M(t)								
t = 5								
PRB	-0.2	0.0	0.4	0.0	3.8	-1.2	3.5	-0.6
SE	0.5	0.1	0.6	0.1	0.9	0.1	1.0	0.1
CIC	85.6	91.1	90.6	93.7	79.8	78.1	89.0	87.4
t = 10								
PRB	-0.2	0.0	-0.1	0.0	-6.4	0.0	-0.8	-0.1
SE	0.3	0.1	0.2	0.1	0.3	0.1	0.3	0.1
CIC	87.4	95.3	92.4	92.7	74.6	95.3	90.7	90.6

1982). Reduction of time variation, particularly if the Lincoln-Petersen estimator is used, is important, but not as critical (Menkens 1987, Menkens and Anderson in press). Again, reducing variation in capture probabilities leads to estimates that have lower bias and increased precision.

Methods for reducing variation in capture probabilities are numerous (see Otis et al. 1978, Seber 1986, White et al. 1982). Behavioral responses may be reduced by the use of different capture and recapture techniques. For example, animals could be captured using live traps and marked, and then "recaptured" visually using spotting scopes. (Fagerstone and Biggins 1986). In addition, use of traps not avoided by animals, and use of non-intrusive marking techniques (e.g., ear tags instead of toe clipping) may also help reduce behavioral responses. Use of traps not avoided by animals may help increase capture probabilities. If sample sizes are large, heterogeneity may be reduced by stratifying the data into sex and age groups with separate analyses performed on each group (Otis et al. 1978, White et al. 1982). If data are stratified however, the effects of small sample size on the estimator's properties must be considered.

Capture probabilities may be increased and their variation reduced after study completion by pooling individual trap periods into single marking and recapture periods as was done in our simulations (Menkens 1987, Menkens and Anderson in press). When data are pooled in this

way and the Lincoln-Petersen estimator used, capture probabilities are 20 to 25% higher than those for individual days (Menkens 1987). In most cases, data pooling results in estimates with improved properties.

Use of the wrong model for analysis leads to estimates with unknown degrees of bias and unacceptably large or unreasonably small standard errors (Otis et al. 1978, White et al. 1982), thus contributing significantly to measurement error. In this study, we forced CAPTURE to use the correct model for analysis. This, is unrealistic however, in that biologist never know which model is appropriate. CAPTURE provides a objective model selection procedure, however this procedure works poorly with the small sample sizes typically encountered in many field studies (Menkens 1987, Menkens and Anderson in press, Otis et al. 1978, White et al. 1982). In most cases, the Lincoln-Petersen estimator is a valid alternative to CAPTURE when sample sizes are small, except when capture probabilities are influenced by severe behavioral responses or large degrees of individual heterogeneity (Menkens 1987, Menkens and Anderson in press). Because use of the most appropriate model is critical, CAPTURE should be used to determine the type and magnitude of capture probability variation in a data set, and if variation is low, the Lincoln-Petersen estimator should be used in analysis (Menkens and Anderson in press).

Many additional factors contribute to measurement error. Eliminating

these requires detailed knowledge of species behavior and ecology, and use of compatible techniques. For example, baits identical to, or that closely approximate natural food items, should be used (Dobson and Kjelgaard 1985). Tags that are easily lost will lead to severe overestimates of population size and should not be used. Other factors that could contribute to measurement error include use of traps or other activities that decrease survival or increase emigration or immigration, and use of improper traps for the species.

Sampling error is the error that results from natural variation between sampling units; the larger this variation, the larger the number of units that must be sampled to detect a difference in population size. For example, when environmental impacts are being assessed, sampling error would be decreased by increasing the number of grids in the control and experimental groups. Reducing variation in capture probabilities allows decreasing the number of days each grid is trapped without large increases in bias or standard errors or decreases in confidence interval coverage rates. By reducing the trap period, more grids can be sampled in a shorter period of time, thereby reducing sampling error and improving the estimate of overall population size. Trapping in as short a time interval as possible will also decrease variation caused by temporal population effects.

One approach to reducing sampling error is to reduce intergrid variation by using a stratified sampling approach. In this case, investigators could stratify the habitat based on some characteristic that is correlated with animal density and trap within these strata. Sample sizes would be estimated for each strata.

Conclusions

Reduction of capture probability variation and maximizing their mag-

Table 3.—The percentage of times the Lincoln-Petersen estimator (LP) or the appropriate CAPTURE model (CAPTURE) was selected by CAPTURE's model selection routine (from Menkens 1987). Model refers to the CAPTURE model under which the data were generated.

Estimator	Model				
	M(o)	M(h)	M(b)	M(bh)	M(t)
LP	96	98	93	99	97
CAPTURE	100	9	7	11	6

nitude are critical to obtaining unbiased and precise estimates of population size, and also allow the selection of the proper model for use in analysis. Although we have concentrated on small mammals, our points concerning reduction of both variation in capture probabilities and of measurement and sampling error, pertain to other studies using mark-recapture techniques (e.g., papers in Ralph et al.). Our conclusions will hopefully force investigators to realize that their techniques, particularly in poorly designed and carelessly performed studies, may not provide as detailed and profound conclusions as they might expect. We reiterate that care in designing a study can minimize many (but not all) of the sources of measurement and sampling errors we have discussed.

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The Design and Importance of Long-Term Ecological Studies: Analysis of Vertebrates in the Inyo-White Mountains, California¹

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A fundamental question that should arise early in the design process of any investigation is the duration of study. Along with questions of sampling methods, sample size, seasons of study, and the like, is the central question of how long to collect data: is 1 week or 1 month ample? Or should the study extend for 1 or more years? Naturally, this is a study-specific question based largely on the objectives of the research. As I show in this paper, however, a study of insufficient length may fail to attain its objectives regardless of the strength of the design components (e.g., sample size). Unfortunately, the researcher and manager may not even realize that the study gave only a partial picture of the system under study; this, then, raises the issue of study length.

As outlined elsewhere (e.g., Likens 1983, Wiens 1984, Strayer et al. 1986), a tradition has developed over the past several decades—especially among North American scientists—of the pursuit of short-term studies. This situation arose from constraints imposed by funding duration, the need to finish graduate programs

within short periods of time, the pressure placed on researchers to publish, and, of course, human nature. A quote from John A. Wiens (1984) in his review of long-term studies in ornithology is appropriate here: "...an excessive preoccupation with short-term studies can lead to short-term insights. By restricting the duration of investigation, we adopt a snapshot approach to studying nature. We can only hope that the glimpses of patterns and processes that we obtain depict reality accurately and that something critical has not been missed because we looked at the system too briefly." These final thoughts—that the pattern we saw may not depict reality, and that a critical factor may have been missed—have direct implications for the design of future wildlife-habitat relationships studies. Such studies are usually of only 1-3 years in duration. At best, they give only a partial view of most ecological systems; and, at worst, lead to false interpretations.

My objectives in this paper are (1) to compare and contrast short- and long-term studies, including discussion of when each type of study can be most useful; I will draw heavily from the comprehensive review of long-term ecological studies by Strayer et al. (1986). (2) Using a study recently implemented in the Inyo-White mountains of eastern California, I will suggest a design for long-term studies that seeks to determine

Abstract.—This paper reviews the importance of duration in the design of studies of wildlife-habitat relationships. Long-term studies are especially suited to examining slow processes, rare events, subtle processes, and complex phenomena. Four major alternatives to long-term studies—retroactive studies, substitution of space for time, use of systems with fast dynamics as analogues for systems with slow dynamics, and modeling—are discussed. All studies should justify their results and (especially) conclusions—recommendations with regard to study duration. A suggested design for a long-term study of small vertebrates is presented, including preliminary data (as an example) from the Inyo-White Mountains of eastern California.

trends in abundance and habitat relationships of small vertebrates.

LONG-TERM STUDIES

Conceptual Framework

As summarized by Strayer et al. (1986), long-term studies are especially suited to exploring four major classes of ecological phenomena: slow processes, rare events, subtle processes, and complex phenomena.

Slow Processes

Long-term studies obviously can contribute to the understanding of ecological processes that exceeds that gained from studies of only 1-3 years in duration. The importance of this contribution depends on the magnitude of the process: results obtained from any several-year period of the hypothetical 25-year curve (fig. 1A) could differ substantially from other periods (e.g., showing an increasing or decreasing trend). Data obtained during any short period could be accurate, but only for that period. Although continuous sampling may not be necessary to identify such a relationship, certainly regularly-repeated sampling is. Prominent examples of such slow processes given by Strayer et al. (1986) are forest succession, invasion of exotic species, and verte-

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brate population cycles. Several specific examples of obvious long-term relationships or cycles are given in Halvorson (1984): the 23-fold difference between peaks and low numbers of snowshoe hares (*Lepus americanus*) during a 15-year study by Keith (1983); and it took 12 years for a relationship between conifer seed-crop and red squirrel (*Tamiasciurus hudsonicus*) abundance to be repeated (Halvorson, unpubl. data).

Rare Events

Ecological phenomena can occur at regular intervals (fig. 1B); such events include catastrophes (e.g., fires, floods), population eruptions, and various environmental "bottle-necks" or "crunches." Shorter-term studies are often used to study such events after their occurrence, focusing on the response or recovery of the system. Studies of post-fire succession (e.g., Bock and Lynch 1970, Raphael et al. 1987), and changes in bird populations following oceanic El Nino conditions (e.g., Barber and Chavez 1983, Schreiber and Schreiber 1984), are a few examples. Short-term studies, cannot, however, be used to study the frequency and reason (context) for the event.

Subtle Processes

Here Strayer et al. (1986) identified processes that change over time in a regular fashion (e.g., monotonic change, a step-function), but where the year-to-year variance is large relative to the magnitude of the longer-term trend (as depicted in fig. 1C). According to Strayer et al., "A short-term study will be unable to discern the long-term trend, or, even worse, will suggest a completely incorrect conclusion about the magnitude and direction of the change...A short-term record simply lacks the statistical power to detect subtle long-term trends..."

Complex Phenomena

Evaluation of biological phenomena are often complicated by the intercorrelated nature of associated environmental factors. Further, relationships between dependent and independent variables may be characterized by both linear and nonlinear responses (e.g., Meents et al. 1983). Long-term data are often necessary to sort out such relationships for several reasons. First, it may simply take many years for the phenomenon to reveal enough of its characteristics to allow meaningful analysis (e.g., to model the system). Further, it may be necessary to accumulate data for many years to provide the necessary statistical degrees of freedom to conduct complex analyses (e.g., multivariate statistics; Strayer et al. 1986).

Other Considerations.—A myriad of other, often related, factors indicate the need for long-term studies. Many of these factors are related to the basic—albeit complex—biology of the organism. Vertebrates have long generation time and long life spans, which tends to mask a population response to environmental change. Site fidelity, another common characteristic of adult vertebrates, may cause a time-delay in the response of an animal to perturbation.

How Long is Long-Term?

Strayer et al. (1986) gave two, rather different, definitions to the concept of "long-term." The first definition considers the length of study in terms of natural processes. Quoting them, a study is long-term "...if it continues for as long as the generation time of the dominant organism or long enough to include examples of the important processes that structure the ecosystem under study...the length of study is measured against the dynamic speed of the system being studied."

A different approach is to view the length of studies relatively, with

long-term studies being those that have continued for a longer time than most other such studies. By following this definition, we are accepting human institutions and constraints (e.g., human life span, length of graduate education, pressure to publish), and not the rate of natural processes (Strayer et al. 1986).

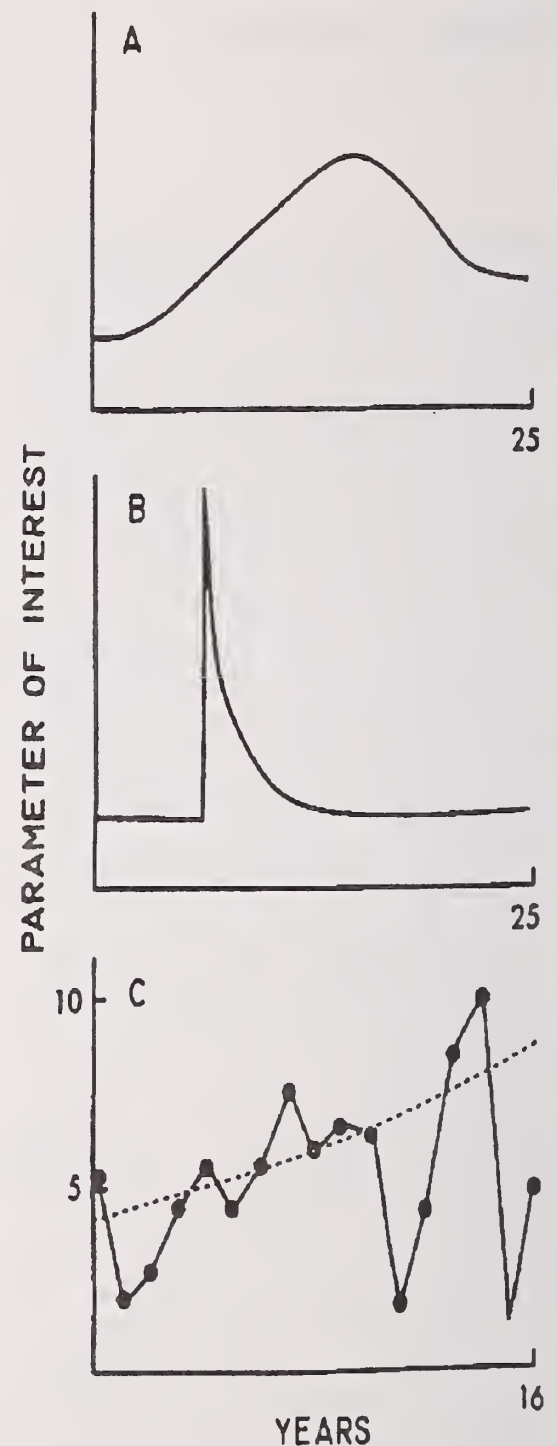


Figure 1.—Situations where long-term studies may be useful. (A) slow processes, (B) rare events, and (C) subtle changes. The record in (C) is a long-term trend beginning at $Y = 4$ and increasing at 5% per year (dotted line) to which a random error with a variance equal to the trend line has been added. Redrawn with permission following Strayer et al. (1986: fig. 3).

To illustrate the difficulty in defining the length of time necessary for a study to be considered long-term, Strayer et al. (1986) contrasted the classic experiment on competitive exclusion in *Paramecium* with the forest ecosystem studies at the Hubbard Brook Experimental Forest: Gause took about 20 days to elucidate the dynamics of the *Paramecium* system; the recovery of a forest ecosystem from clearcutting has been underway for 20 years, which is perhaps only 1/20 of the time necessary for the forest to reach steady-state. By the first definition, Gause's work is long term, while the 20-year Hubbard Brook work is not; the latter becomes "long-term" under the second definition.

Thus, one cannot establish a formal definition for "long term." Researchers should recognize, however, that conclusions drawn from any study should consider the dynamic speed of the system being studied. As reviewed by Likens (1983), there are numerous examples which illustrate that 5 to 20 years of baseline data are required to characterize the complexity of ecological interactions and systems.

Length of Study: Advantages and Disadvantages

Not all studies must be "long term" to provide reliable results. Descriptive studies of essentially static patterns (e.g., morphology, genetic characteristics of species), of processes at the individual level (e.g., growth, behavior), or evolutionary patterns or systematic relationships do not necessarily require long-term study. These phenomena occur on time frames that are either very short or very long relative to the normal duration of a short-term study (Wiens 1984). The principal disadvantages of long-term studies are not ecological, but practical. The need for continued support of money, time, staff, and facilities; the problems associated

with the study falling into unproductive complacency; and environmental concerns that often require immediate, even if incomplete, answers.

As pointed out by Wiens (1984), long-term studies, because of the intense and continued commitment of time and money, must focus on just a few specific situations. Long-term work, therefore, must sacrifice the breadth possible with a series of short-term studies, in exchange for this increased detail and intensity. This, of course, reduces the potential for generalizing from such (long-term) studies. A degree of compromise between these extremes (short-term vs. long-term studies) is discussed below.

Alternatives to Long-Term Studies

There are four classes of short-term studies that can potentially provide insight into long-term phenomena: (1) retrospective studies, (2) substitution of space for time, (3) use of systems with fast dynamics as analogues for systems with slow dynamics, and (4) modeling (Strayer et al. 1986). They raise the important point that such short-term approaches can be integrated into an overall, longer-term, study, thus "...extending the temporal and spatial scales of the investigation and allowing the ecologist to explore a wider range of ecological phenomena than might be practical in a direct long-term study."

Retrospective Studies

The record of past conditions can be used to help reconstruct a long-term trend. Obvious examples of such approaches are tree-rings and pollen deposition. Unfortunately, conclusions regarding past conditions related to or even causing the pattern remaining can only be inferred; further, only persistent structures remain to be analyzed.

Substitution of Space for Time

This is an often-used substitute for a long-term study. Here sites with differing characteristics are used instead of following the course of a single or a few sites for an extended period. For example, evaluating succession by simultaneously using sites of different age (e.g., 1, 5, 15, 30 years post-harvest). This approach, however, requires the assumption that all important environmental processes are independent of space and time (i.e., all sites must have the same environmental characteristics and history). To provide valid results through this approach requires, then, that many sites with very similar histories and characteristics be used. An obvious problem, of course, is determination of how "similar" sites must be. Although results of such studies may theoretically approach those of a long-term study, they can only do so with a large number of replicates. Further, such substitutions cannot capture the historical events that shaped each site, but can only mask or "swamp" the effect through a large sample size (which may yield adequate results for many applications).

These problems can best be dealt with in studies combining direct long-term studies with space-for-time substitutions. Long-term studies done in parallel with carefully matched, short-term "substitutes," can factor out the year-to-year variation that may mask general trends.

Other Methods

Applying the results of a simple system with rapid generation time can give insight into how a system with a slower generation might behave: for example, applying the results of laboratory studies on rodents to evaluations of population dynamics of larger mammals. Such extensions of results have obvious drawbacks, but can be useful in the development of general theories used to guide

longer-term studies.

Mathematical modeling can, of course, be used to predict the longer-term behavior of a system. Such models are often based on guides provided by various short-term studies. Obviously, the predictive ability of models can only be determined through long-term studies, and/or a series of short-term perturbations that experimentally test them; the latter will fail unless all likely catastrophes and conditions can be adequately simulated. Here again, such modeling can provide valuable insight into the design and conduct of parallel long-term studies.

Ecological Monitoring

Monitoring of environmental conditions is a closely aligned aspect of long-term studies. When a management agency such as the USDA Forest Service discusses the need for monitoring of wildlife population numbers, they are essentially describing a long-term study, the goal of which is to identify trends. Unfortunately, "monitoring" has a low status in ecology, being widely regarded as possessing little originality and as unproductive of new scientific knowledge (Strayer et al. 1986). Monitoring data can provide, however, essential support for many research projects and publications arising from long-term studies. In addition, monitoring programs can lead to important and unexpected discoveries (e.g., first report of acid rain in North America; Strayer et al. 1986).

Sutcliffe and Shachak (in Strayer et al. 1986) outlined several elements that are essential in the conduct of monitoring programs: (1) the initial sampling design, variables to be measured, and methodology must be carefully chosen; and (2) a scientist capable of interpreting the data should be closely involved with all aspects of the study, allowing modification of design to take advantage of the ever-increasing knowledge

about the system under study. A critical aspect of any monitoring program is to eliminate the unproductive parts of the program to allow for more fruitful analyses without destroying some part of the long-term core data (Strayer et al. 1986).

STUDY DESIGN

Introduction

The design of a long-term study must be sufficiently simple to persist over a long period of time. Thus, essential measurements must be simple enough to be repeatable by workers with varying degrees of experience (Strayer et al. 1986). There are also numerous specific aspects of site protection and management, management of data, quality control, changing methodologies, and the like that are all critical to a successful study; these concerns are discussed by Strayer et al. (1986) and will not be repeated here.

The design of a long-term study must also be sufficiently flexible to accommodate short-term investigations. Long-term data often suggest questions that can be investigated through short-term experimentation or observations. A benefit of such an approach is that overall productivity can be increased; the longer-term objectives of a study can also be more easily funded as a result of such shorter-term efforts. In summary, studies of varying lengths can usually complement one another.

I have designed and implemented a study to evaluate both short- and long-term responses of vertebrates to abiotic and biotic conditions in the Inyo-White mountains (Inyo and Mono counties) of eastern California. The design represents a compromise among the many different methods necessary to sample different groups of small vertebrates on the same site. Below I briefly describe the sampling design, and provide data on initial surveys. I present this design as a

possible template for other studies that seek to determine wildlife-habitat relationships and responses to environmental changes (i.e., monitoring) over the short- and long-term.

Rationale

The overall objective of this study is to determine long-term behavioral and ecological attributes and interrelationships of vertebrates in the Inyo-White mountains of eastern California. Amphibians, reptiles, small mammals, and birds will be censused on a series of sites in the pinyon-juniper (*Pinus monophylla*-*Juniperus osteosperma*) plant community on a year-round basis. Abiotic factors and food resources will also be sampled. Reproductive physiology of small mammals will be addressed.

Numerous hypotheses can be evaluated depending upon the taxonomic group(s) (e.g., species level, class level, guild level) chosen for analysis; for example:

1. H_01 : The population numbers of the group are not related to (a) food resources, (b) abiotic conditions, and/or (c) population numbers of other groups.
2. H_02 : The behavior (e.g., foraging behavior) of the group does not vary with fluctuations in (a) food, (b) abiotic conditions, and/or (c) population numbers of other groups.
3. H_03 : Population numbers of the group during spring are not related to (a) food, (b) abiotic conditions, and/or (c) number of other animals during a previous season.
4. H_04 : Guild structure cannot be identified on any temporal basis.

- 4a. H₀4: The guild structure identified does not vary with variation in (a) food, (b) abiotic conditions, (c) population numbers of other groups, and/or (d) temporally.

This study is designed to address these and numerous other null hypotheses. The data set necessary to answer any one hypothesis is very similar to that required to address another hypothesis. Thus, the number of hypotheses generated is, in a sense, independent of the effort expended to collect the data.

This study will contribute to our understanding of the ecology of this system in several major ways. First, it will provide data on fluctuations in population numbers of vertebrates, thus serving a monitoring role (especially important to the USDA Forest Service). Second, it will provide data which will allow development of multi-species population models (by myself and other workers), allow development of habitat-relationships models that incorporate both short- and long-term responses to biotic and abiotic factors, and allow development and subsequent testing of models of multi-species interrelationships at various taxonomic levels. Third, and possibly the most important aspect of the study, it will result in the accumulation of vast amounts of ecological information on the vertebrate (and invertebrate) community. To date, only brief and sporadic surveys have been conducted in the Inyo-White mountains. Finally, it is my goal to use preliminary results to generate specific hypotheses that can be tested by my, or others', students. For example, if initial data indicate rejection of the null hypothesis of no relationship between a certain small mammal and their prey base, then a student could select additional sites where food supplementation and/or removal experiments could be conducted. Additional, study-specific funding will be sought for such studies. This study will thus generate

short-term results under the general framework of its long-term design and goals.

The Inyo-White mountains were chosen as the study location for several reasons. First, my intent was to select a type of habitat that offered structural, especially vertical, diversity intermediate between that of a grass- or shrubland and that of a mature, hardwood or coniferous forest. With a canopy rarely exceeding 10 m, I will be able to sample arthropod populations from the upper canopy. This is not conveniently possible in mature conifer forest, where the canopy extends to 20-30 m or more in height. Second, I desired an area that offered only several dominant tree and shrub species: this allows intensive sampling of all major species, while allowing some diversity of plant species beyond that evident in more monotypic habitats.

The pinyon-juniper woodland was chosen because of its extensive coverage throughout the intermountain west. Further, the pinyon-juniper woodland undergoes few significant changes in plant species frequency and density relative to earlier successional communities. Austin (1987), for example, showed virtually no change in a pinyon-juniper community in Utah between 1974-84. In contrast, seeds and berries undergo often marked, interyear changes in production. Thus, barring some catastrophic change, the gross composition of the plant community used in this study should remain relatively stable, helping to control for at least some of the variance likely to be encountered in animal communities.

A definition of what I mean by "long-term" in this study is not yet possible, but I have committed myself to this study for an indefinite period; 15-20 years seems a minimum. The study is designed to be conducted, at a minimum, by myself and one assistant. Additional personnel, primarily undergraduate volunteers during summer, will also be available. Thus, the ability to adequately

conduct the study over the long-term is considered in the design, and will be possible given my focus (concentration) on this study. The initial design can accommodate expansion in size both through the enlargement of each site (using the original area as a standard core), and/or the addition of additional sites (e.g., to sample from a wider range of ecological conditions). Various ancillary studies will add to my understanding of this system, although my primary goal is to examine the interrelationships among vertebrates and their environment.

Sampling intensity will not be increased beyond that discussed herein (see Methods) to avoid substantial impact (e.g., trampling) by observers on the study sites. Thus, an increase in effort (given adequate time and funding) will be directed towards an increase in site size, number of sites, and/or towards ancillary studies, the decision based on preliminary data.

I will be intensively involved with all aspects of this study, including establishment of the sites (already accomplished) and collection of data throughout the duration of the study. It is essential, in any long-term effort, that methodology be standardized, and a high level of quality control be maintained. My involvement will serve as the standard upon which new assistants will be trained. Any changes in methods, whether this involves modification of sampling intensity or a change in trap type, will be fully documented. If any procedures must be changed, the old and new methods will be run simultaneously to allow for intercalibration of methods (as described by Strayer et al. 1986). All field notes and data will be duplicated or triplicated and stored in several locations for safety.

Design Considerations

The study sites—their number, size, and location—chosen for this study were selected to restrict samples to

convenient and modest-sized populations. They will be low in cost to sample and are located in practical locations for year-round access. With the few (3) sites chosen, it would be foolhardy to attempt representation with probability sampling of entire populations. The study is designed to spread effort across important variables to obtain some measure of confirmation of results. I follow the philosophical view of Popper (1959), as summarized by Kish (1987): "The choice of the sites should strain to increase the possibilities for falsification." Similar and consistent results from the replications yield stronger confirmation than a single site would. But if the results are discordant, the replications are too few to yield dependable inference; then further research is indicated. Discordant results yield a healthy skepticism that naive "success" from a single site would obscure (taken from Kish 1987). As discussed earlier, the study is designed to allow an increase in the number of sites (or their size, etc.) should early results so indicate.

The general locations of the sites were not chosen at random. A general area was identified based on (1) ease of access during winter (e.g., within 0.5-1.0 km of a maintained, although usually dirt, road), but also (2) isolated from access by off-road vehicles. Using these general guides, specific sites were chosen to represent a sampling of slope, aspect, and longitudinal location in the Inyo-White mountains. My intent was to increase the likelihood of "falsification," which is better served with tests obtained in contrasting conditions, as opposed to selecting more or less "average" sites (see Kish 1987 for a development of this strategy). The extremes of a relationship are more informative than either random or modal or centralized selection. Three sites were considered a minimum, because two sites might indicate a false, linear relationship in certain factors. Survey data will be collected on other areas throughout the

Inyo-White mountains. Such data will provide useful information regarding the overall distribution and habitat associations of vertebrates throughout the ranges. Further, these sites will serve as "back-ups" should a catastrophic event occur on one of the three main sites. Because this study is largely exploratory, such a strategy was warranted (with the option of later expansion).

METHODS

Terminology

I have attempted to standardize the terms used to describe the study areas described beyond; they are:

"Permanent site": a 400 x 400 m (16 ha) area that forms the long-term "study sites" used.

"Point": a trap location within a site.

"Ancillary site": additional areas (of various shapes and sizes) sampled at an intensity less than on the permanent sites; established to increase scope of sampling effort.

"Sampling period": a 5-7-day period in which a permanent site is sampled.

"Transect": the parallel, 400-m long lines ("transect") forming the study sites.

"Core trapping area": the central, 200 x 200 m area, location within a study site where small-mammal and pitfall traps are placed.

Sampling Schedule

Study sites (described below) were established during fall 1987. All methods outlined herein were evaluated during fall 1987, winter 1987-88, and spring 1988. Each permanent site will be visited for a 5-7-day period on two occasions per season. Seasons are defined as: spring (1 Mar.-31 May); summer (1 June-31 Aug.); fall (1 Sept.-30 Nov.); and winter (1 Dec.-28 Feb.). The exact length of visit will

be based on trapping results. Initial order of visit to sites will be randomized; this order then followed on the subsequent visit in that season.

Remaining time available during a season will be spent sampling the ancillary sites. These ancillary sites will increase my knowledge about the distribution and relative abundance of vertebrates and invertebrates in the Inyo-White mountains. Not all data from ancillary sites will be directly comparable—to permanent or other ancillary sites—because of the lower sampling intensity. Nevertheless, they will supply information important to the long-term success of the study.

Permanent ($n = 3$) Study Sites

Each will be established as a 400 x 400 m (16 ha) site. A 16-ha site was chosen because: (1) an observer can travel this distance, even over rough terrain, in a short period of time; (2) the utilized area of most small vertebrates can be sampled within a 16-ha area; and (3) this area allowed establishment of sites protected from roadways, trails, and other human activity (e.g., fit between cliffs and gullies that form barriers to illegal vehicle access). Each site will be sampled repeatedly within a season to provide measures on within-site variability. The effective n per permanent site is, of course, one (for comparison among permanent sites, $n = 3$). Each site will have permanent grid points marked at 25- or 50-m intervals (using rubber cattle ear tags).

SAMPLING

Amphibian, Reptile, and Small-Mammal Trapping

One-hundred-one Sherman live traps and 41 pit-falls (two 3.2 l (3 lb) tin cans taped together) were established on each site. Live traps were

12.5 m apart in the center 100 x 100 m section of a site, and at 25-m spacings in the remaining trapping area. The closer trap spacing helps determine actual population density, whereas the wider spacing in the surrounding area provides information on animal movements.

Live traps are baited with seed mixtures and checked each morning and late afternoon. Certain rodents (e.g., *Peromyscus*) are active throughout the year. During winter, therefore, traps are provided with insulating material (e.g., wool). All captures are toe-clipped. Trapping continues until new captures are minimal (usually 5 days). Pitfalls are not baited, but captures are marked and released. Traps are run "dry": holes were drilled in each trap, rocks placed in the bottom of each hole to provide drainage, and a wooden lid placed over the trap to reduce exposure.

Bird Activity

The spot-map method (e.g., see Ralph and Scott 1981) is used to determine bird abundance and territory (during breeding) size. Following a census, the observer slowly walks though the entire site and records foraging birds as encountered. Data are recorded on activity and substrate used. (The specific methods used for birds will not be detailed in this paper.)

Vegetation Sampling

General site

Trees and shrubs will be sampled once per year, and grass and herbaceous cover will be sampled once per season. Changes in plant phenology will be recorded as they occur. Vegetation will be sampled using circular plots and line intercepts centered at each of the 81, 50-m-transect intercepts. Pinyon and juniper will be

counted and measured (e.g., dbh, height, vigor, canopy cover) within 20-m-radius plots. Shrubs, grass, and herbaceous cover will be measured along 40-m-long line intercepts bisecting each circular plot (and running parallel to the main transect line).

Trap Locations

Vegetation and soil characteristics will be measured at each trap site. The nearest tree in each quarter from the trap will be measured. Two 5-m-perpendicular transects will be placed over each trap; shrub and herbaceous cover will be measured along each transect. Soil moisture, compactability, texture, and pH will be measured on each arm (2.5 m) of the trap-site transects: at 0.5, 1.0, 1.5, and 2.0 m (one of these distances per arm, randomized, for four measurements per trap). These samples will be gathered once during each season.

Abiotic Factors

A weather station will be established near the center of each study site. Temperature, humidity, and rain fall will be automatically recorded throughout the year. Snowfall will be measured by visiting each site following snowstorms.

Other Sampling

Data on arthropod abundance (branch sampling and pan traps) and cone-seed production (of pinyon, juniper and major shrub species) will also be collected (but not detailed in this paper).

RESULTS

Only one site has been sampled with adequate intensity for presentation of data at this time. Sampling occurred

during fall (8 days during two trapping sessions), winter (7 days during two trapping sessions), and spring (12 days during three trapping sessions). Pitfalls were used only during the first trapping session in the fall and the last session in the spring (because of snow and little or no lizard activity). Chipmunks and Great Basin pocket mice were not active from October-November until early March.

The sagebrush and western fence lizards were the most frequently captured animals in pitfalls (table 1). A single deer mouse (immature) was also captured in a pitfall trap. Intensity of pitfall trapping has been inadequate to date to make conclusions on their effectiveness.

Seven small mammal species and a skink were captured in the live traps (table 1). The pinyon mouse was the most abundant species captured during fall. Relatively few pinyon mice were captured during winter, however (a 77.9% decline between fall and winter). The decline of pinyon mice continued into spring, with abundance dropping 64% between winter and spring. Only a few deer and pinyon mice were captured during winter.

The highest overall abundance of small mammals was found during spring (table 1). The two species of chipmunks were the most abundant animals captured. The Great Basin pocket mouse and the deer mouse were also captured frequently during spring.

DISCUSSION

Live-trapping data indicate the importance of repeated sampling over time: pinyon mice apparently suffered substantial winter mortality. Thus, trapping in only fall or spring would have falsely indicated a relatively high or low population size, respectively. Although this study can hardly be considered "long-term," initial results do highlight the need

for repeated sampling even over the short term. Only continued sampling will elicit the frequency and reasons for such a decline. My initial trapping configuration contained a dense trap placement (12.5 m trap intervals) in the middle of the grid relative to the outer traps (25-m spacing). My intent was to use the outer traps to determine movement of animals in and out of the smaller 100 x 100 m area. cursory examination of trapping results (unpubl. data) indicate, however, that even the total 200 x 200 m grid is not sufficiently large to quantify movements (i.e., animals moving >200 m). Therefore, I suggest the following modifications in trap placement: 10 x 10 trapping grid with 15-m spacing. This placement should adequately sample the animals present. To detect movement (e.g., dispersal), trap lines can be established periodically that run perpendicular from the edge of the trapping grid.

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Table 1.—Abundance (no./100 trap-nights) of reptiles and small mammals, Inyo-White mountains, California, during fall (Sept.-Nov.) 1987, winter (Dec.-Feb.) 1987-88, and spring (Mar.-May) 1988.

Species	Fall ^a		Winter ^b		Spring ^c	
	Captures	Abund.	Captures	Abund.	Captures	Abund.
Western fence lizard (<i>Sceloporus occidentalis</i>)					2 ^d	1.4
Sagebrush lizard (<i>S. graciosus</i>)	1 ^d	1.3			3 ^d	2.0
Gilbert skink (<i>Eumeces gilberti</i>)					1 ^e	0.1
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)					1	0.1
Least chipmunk (<i>Eutamias minimus</i>)	3	0.4			39	3.2
Panamint chipmunk (<i>E. panamintinus</i>)					41	3.4
Great Basin pocket mouse (<i>Perognathus parvus</i>)					29	2.4
Deer mouse (<i>Peromyscus maniculatus</i>)	9	1.2	12	1.7	26	2.2
Pinyon mouse (<i>P. truei</i>)	56	7.7	12	1.7	7	0.6
Desert woodrat (<i>Neotoma lepida</i>)	1	0.1				
Total	69	9.5	24	3.4	143	11.8

^aTrap-nights: 75 for pitfalls, 728 for small-mammal traps.

^bTrap-nights: 0 for pitfalls, 707 for small-mammal traps.

^cTrap-nights: 147 for pitfalls, 1211 for small-mammal traps.

^dCaptured in pitfall.

^eCaptured in small-mammal trap.

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An Ecological Problem-Solving Process for Managing Special-Interest Species¹

Henry L. Short² and Samuel C. Williamson²

Abstract.—We present a structured problem-solving process that can help resolve wildlife management issues. Management goals for wildlife species are expressed in terms of populations to be attained and maintained. Habitat quantity and quality necessary to achieve those population goals can then be determined. Proposed land-use changes are evaluated in terms of how they will contribute toward recovery or extinction of the species of interest.

Land-use problems associated with the need to protect wildlife habitat and the desire to develop resources can sometimes be resolved using an ecological problem-solving process. The process requires development of a management goal for individual wildlife species, determination of the quantity of habitat required to achieve that management goal, and an appraisal of how development scenarios will affect the management goal.

We describe how the process might work using available data about the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). The exercise is relevant because the squirrel exists entirely as a disjunct population in the high elevation coniferous forest community of the Pinaleno Mountains of southeastern Arizona, and a new astrophysics observatory has been proposed within important squirrel habitat. Our process was not applied in the development of the Environmental Impact Statement (EIS) prepared for the red squirrel and its habitat nor in negotiations for the future management of the squirrel. An extensive and current infor-

mation base (Spicer et al. 1985; U.S. Forest Service 1987, 1988) recently has been developed for the Mount Graham red squirrel in order to develop the EIS for the proposed astrophysics observatory. We applied these data to a cumulative impacts assessment process being developed by the U.S. Fish and Wildlife Service. We assume that species-habitat management goals can be developed and that these goal statements can drive habitat management plans and activities. We have not analyzed the merits of any development scenarios proposed for the astrophysics observatory.

The Pinaleno Mountains are an isolated range that supports one of the southernmost spruce-fir forests in North America (Spicer et al. 1985). The Mount Graham red squirrel is endemic to the small patches of coniferous forests that occur at the highest elevations of the mountains. The squirrel has been affected by a variety of human activities and natural events that have altered its habitat. Disturbances included completion of a road to the mountain top in 1933, introduction of the tassel-eared squirrel (*Sciurus aberti*) in 1941 to 1943, extensive logging activities in subalpine coniferous forests from 1946 to 1973, a major fire in 1956, and extensive windthrows in the 1960's (Spicer et al. 1985). The squirrel was first collected from the Pinaleno Mountains in 1894 and was considered "common" in the spruce-fir

zone above 2,590 m in 1914. Since the early 1950's it has been considered "uncommon" throughout the coniferous tree zone of this mountain range (Spicer et al. 1985).

THE PROCESS

The problem-solving process used in our analysis contains three principal steps (fig. 1). Problem description, the first step, defines the ecological problem and identifies the species, study area, and time frame of concern.

Problem analysis, the second step, develops biological information necessary to achieve a solution. An initial effort is to describe a management goal for the species of concern in terms of a specific population level to be achieved and maintained. This numerical target is not a vague statement to "maintain" or "enhance" because such terms cannot be used to measure the results of management actions. The management goal should be collaboratively developed so that all interested parties reach a consensus on the desirability for perpetuating the species and on a population level to be achieved by management. It is understood that mutually agreed upon goals represent compromise and that compromises are rarely satisfactory to all concerned parties.

It is then necessary to determine the quality and quantity of habitat

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required to achieve the management goal. This requires building a model describing habitat requirements for the species. An understanding of how human activities and natural events impact habitat quality and quantity is also desirable because the management of these restricting actions may help achieve the management goal for the species. The identification of causes contributing to

habitat deficiencies can be made by interviewing persons familiar with the species and the particular habitat conditions within the study area.

The third step in the process, solving the problem (fig. 1), is accomplished after: (1) the amount and quality of habitat necessary to fulfill the management goal has been determined, (2) the quantity of suitable habitat presently available has been

documented, and (3) the quantity of suitable habitat that would be available under different land-use options has been projected.

Describe the Problem

The Mount Graham red squirrel has probably declined during this century (fig. 2) in part because of the piecemeal degradation of isolated forest habitat. The variety of human activities and natural events causing this decline might soon be augmented by the development of the astrophysics observatory on the Pinaleno Mountains. Can this and related developments occur in a manner that does not further jeopardize the existence of the endangered red squirrel during the foreseeable future?

Analyze the Problem

Determine the Management Goal for the Species

The management goal is described in terms of a population to be attained and maintained. Ideally, population goals should be based on quantitative historical levels of abundance. Population goals are more difficult to establish if historical information about population levels are fragmentary and descriptive, as for the Mount Graham red squirrel. In such cases, criteria for establishing desired population levels should consider: (1) estimates of present populations and trends, (2) threshold values necessary to ensure the survival of the species, and (3) estimates of the potential population level that could be attained if management of an area was accomplished solely to benefit the species.

Estimates of population trends for the Mount Graham red squirrel are largely qualitative (fig. 2). The results of field work suggest that the autumn 1987 population of red squirrel

I. Describe the Problem

II. Analyze the Problem

1. Determine the Management Goal for the Species.
2. Describe Important Habitat Conditions for the Species.
3. Determine how Human Activities Affect Habitat Conditions Important to the Species.

III. Solve the Problem

1. Determine Acceptable Strategies for Managing Habitats Required by the Species.

Figure 1.—Steps of the problem-solving process.

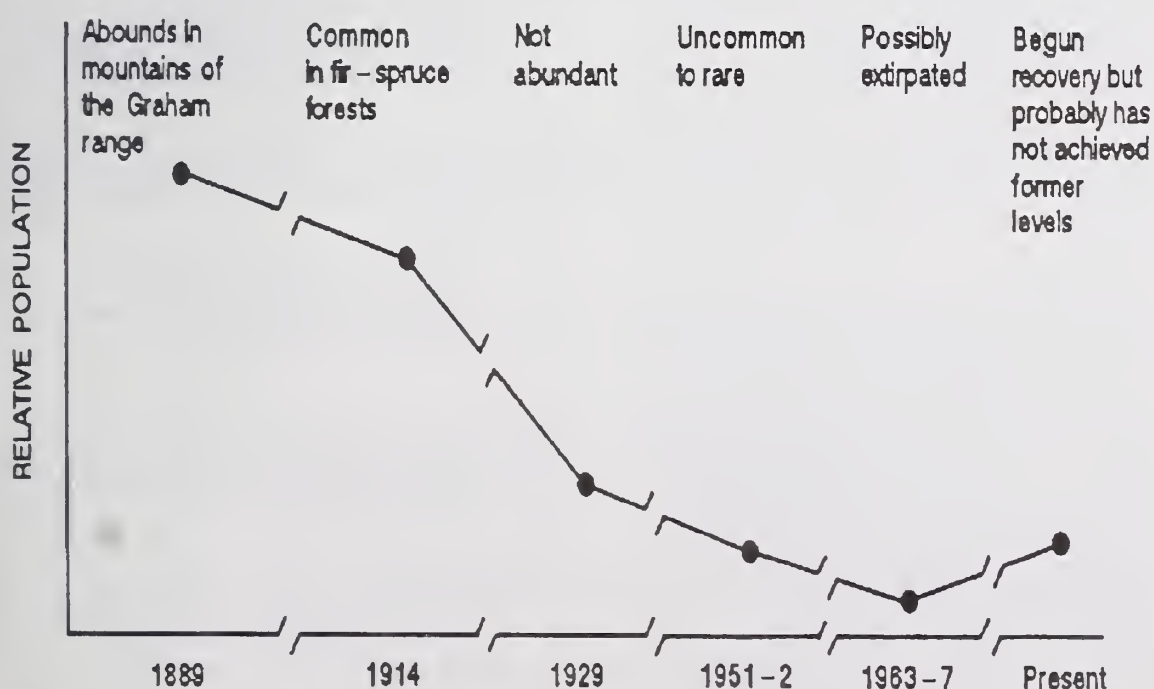


Figure 2.—Possible trends in abundance of the Mount Graham red squirrel. (Population descriptions are those of Spicer et al. 1985.)

rels on the Pinaleno Mountains might be 246 (206-286), (U.S. Forest Service 1988:37). Computer simulations of population dynamics of the red squirrel (U.S. Forest Service 1988:74) are only minimally helpful because data such as natality and mortality for the Mount Graham red squirrel are unknown. The computer simulations suggest probability levels for extinction under different combinations of mortality and reproduction. The predicted carrying capacity for the squirrel under current habitat conditions has been estimated at 502 squirrels. The potential future carrying capacity, based on the quantity and present age structure of mixed conifer and spruce-fir stands, is 725 squirrels (U.S. Forest Service 1988:72-73). Thus, the current population of red squirrels might be somewhat higher than that in the early 1960's when the species was reported as possibly extirpated (fig. 2), but less than one-half the present carrying capacity for the species. The collaboratively developed management goal might state, for example, that the management goal for the species is to develop and perpetuate a red squirrel population equal to the present carrying capacity of the habitat for the squirrel which is estimated at 502 squirrels (U.S. Forest Service 1988:73).

Describe Important Habitat Conditions for the Species

A species-habitat model for the red squirrel can be based on the squirrel's dependency on seed cones and trees that produce those cones. Conifer seeds are the primary food of the red squirrel, which cuts cones in summer and caches them in middens in dense needle litter at stumps, downed timber, and on the base of snags or live trees in forests with dense overstory canopies (Spicer et al. 1985).

We constructed a species-habitat model for Mount Graham red squirrel

rels using data given in the U.S. Forest Service (1987) report. The structural stage, tree species, and canopy density that compose red squirrel habitats are classified as excellent, good, fair, poor, very poor, and no value (fig. 3). These data were developed by U.S. Department of Agriculture Forest Service personnel and others familiar with the habitat requirements of the squirrel and were based on vegetation type and structural stage, the number of snags and downed logs per hectare, aspect, and slope (U.S. Forest Service 1987:44). Midden complexes are a focal point of territories and the number of active middens is supposedly associated with the number of red squirrels in a stand (Spicer et al. 1985). The data for middens per hectare have been adjusted so that a score of 1.0 is listed for excellent habitats, 0.0 for no value habitats, and intermediate values are listed for habitats of intermediate quality (fig. 3).

The species-habitat model describes conditions in habitats of different quality. A simple word model was then developed to describe a unit of good or excellent habitat for a red squirrel (fig. 4). The model developed from information in figure 3 and U.S. Department of Agriculture (1987:33-37) defines suitable habitat for a red squirrel as a 1-ha forested block that: (1) is contiguous to other similar forested blocks, (2) provides a dense overstory canopy of spruce-fir or mixed conifers, and (3) contains about 15 "good" seed-bearing trees per hectare.

Such species-habitat models are general and approximate. Still, they provide an estimate of what comprises a unit of habitat area and condition that might be required by a squirrel. If a management goal is to provide habitat for X red squirrels then that goal can possibly be achieved by providing X units of good to excellent habitat (fig. 4). The need to provide this quantity of a specific habitat condition should drive management plans for the sub-

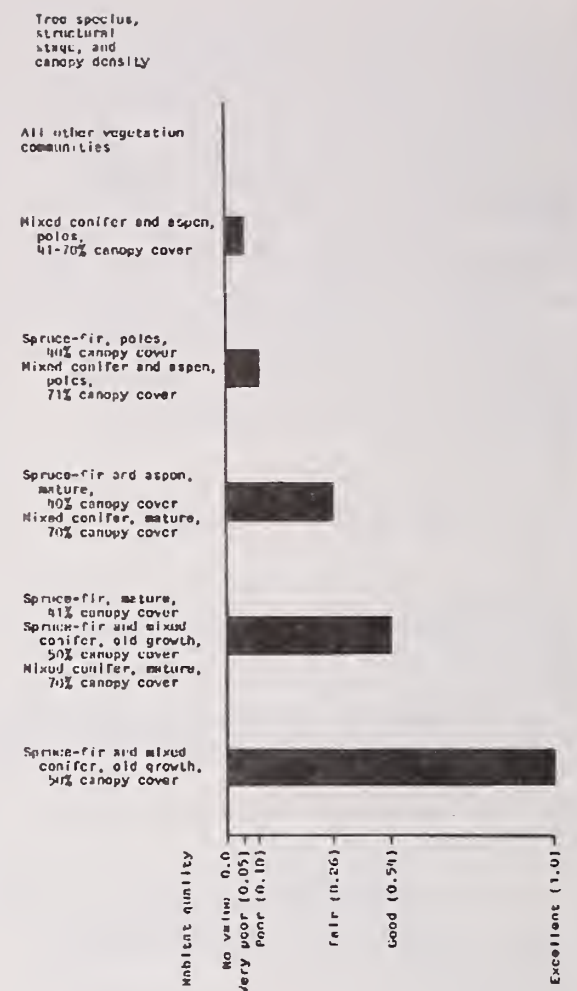


Figure 3.—Habitat quality for the Mount Graham red squirrel can be described in terms of tree species, structural stage, and canopy density within forest habitats. Habitat quality is measured in terms of middens per hectare for different habitats scaled on the basis of 0.0 for no value habitats and 1.0 for excellent habitats. Data from U.S. Forest Service (1988:112).

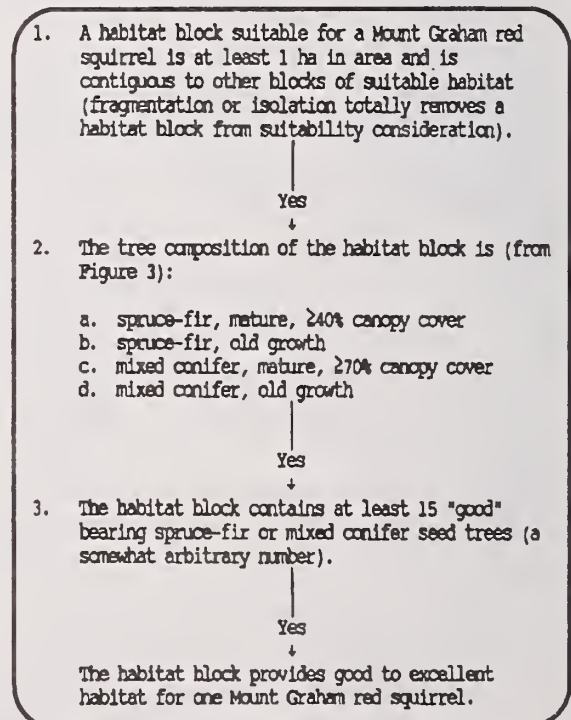


Figure 4.—A word model describing good to excellent habitat condition for a red squirrel.

alpine coniferous forests of the Pinaleno Mountains.

Determine How Human Activities Affect Habitat Conditions Important to the Species

Several human activities and natural events may adversely affect habitats of the Mount Graham red squirrel and reduce the opportunity to achieve the management goal for the species. A listing of possible impacts on the Mount Graham red squirrel and the probable resulting habitat changes is in figure 5.

The cells in a cause-effect matrix (table 1) list estimates of the direction and relative importance of each factor affecting a habitat criterion. The cells within the cause-effect matrix can be completed after synthesizing information from the literature, from

best professional judgments elicited from selected personnel or preferably from analyzing results of appropriate research. Information within the cause-effect matrix can indicate the relative importance of different human activities on squirrel habitats and identify actions to be favored or avoided to help achieve the management goal. For example, habitat fragmentation, clearcutting, selective harvest, and forest management favoring early vegetation successional stages are important negative factors to red squirrel habitats whereas management favoring dense, mature or old-growth stands of mixed conifer and spruce-fir forests are important positive actions, favorable to red squirrels. Causes of negative and positive impacts to species or habitats of concern are factors that should be considered when formulating and evaluating plans for modify-

ing habitats important to selected wildlife species.

Solve the Problem

Determine Acceptable Strategies for Managing Habitats Required by the Species

A way to evaluate the diversity of different land-use scenarios is listed in figure 6. Threshold values describing the quantity of suitable habitat necessary for achieving the management goal for the red squirrel can be represented as habitat condition 2 in figure 6. If the quantity of suitable habitat presently available had exceeded this threshold value (condition 1a) then changes to the quantity of available habitat could be tolerated and that fact could be considered in making a decision about a potential land use.

The present quantity of good to excellent habitat for the red squirrel in the Pinaleno Mountains, however, is probably more closely approximated by condition 1b in figure 6. A variety of conditions like those itemized in table 1 have reduced habitat quality and quantity resulting in a diminished squirrel population with an endangered species listing. A land-use plan that continued impacts (like those listed in table 1) would further reduce the area and quality of contiguous blocks of forest habitat important to the squirrel. Any further fragmentation or degradation of habitat would be expected to further diminish the population (1b1 in fig. 6) and perhaps threaten extinction of the subspecies. A land-use plan that neither allowed further degradation of habitat nor actively improved habitat conditions for the squirrel might result in maintaining present population levels (1b2 in fig. 6). The most desirable land-use scenarios are those likely to produce trend lines such as 1b3 (fig. 6). These land-use plans would minimize fragmentation of habitats and would actively man-

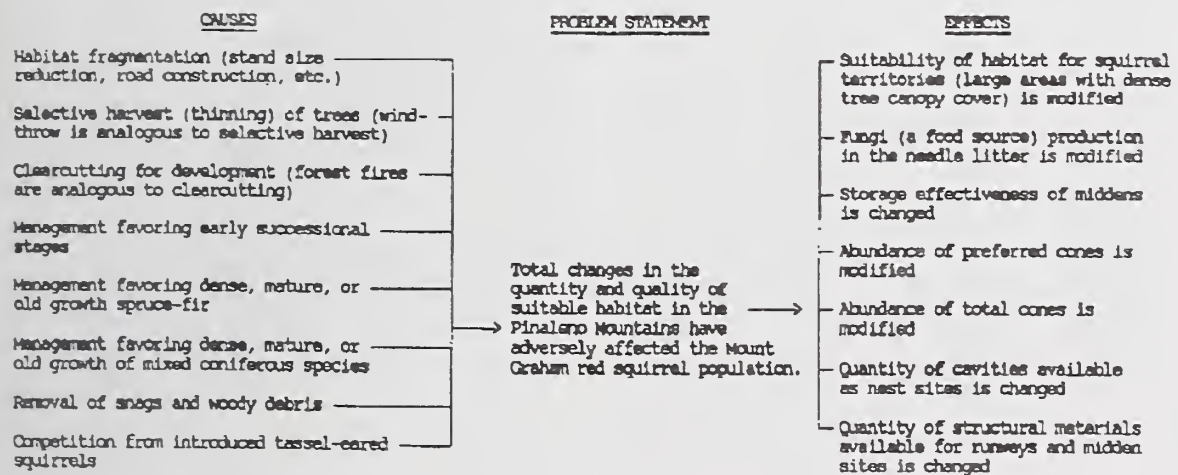


Figure 5.—A cause/effect model identifying causes that affect the quantity and quality of habitat suitable for the Mount Graham red squirrel.

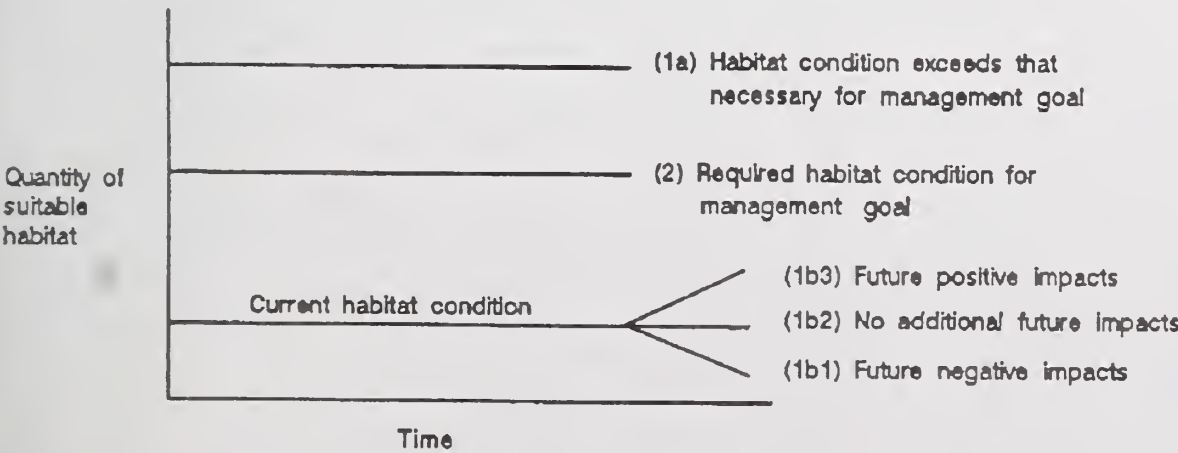


Figure 6.—Habitat conditions under a variety of management strategies.

age habitats to develop large contiguous blocks of old-growth mixed conifers and spruce-fir on the Pinaleno Mountains to help attain the desired population level of red squirrels.

CONCLUSIONS

We emphasize that potential land-use change can be evaluated in a ra-

tional manner if management goals for wildlife resources have been previously established and agreed upon. The merit of this approach is that planning becomes an active rather than a reactive exercise. Too often we evaluate proposed land-use changes in terms of how they might affect present habitats and present populations without considering how present conditions compare to desired

populations and necessary habitats. Without establishing a management goal and determining the habitat conditions necessary to achieve that goal, we could accept the wrong baseline for developing our management strategy (perhaps something analogous to line 1b2 in fig. 6). If this occurs, we might have little success in maintaining viable populations because we frequently strive only to

Table 1.—A cause-effect matrix that lists the relative importance of causal agents (causes listed in fig. 4) that change the quantity and quality of habitat features (effects listed in fig. 4) for the Mount Graham red squirrel. A (+) value indicates a positive impact and a (-) value indicates a negative impact. Numerical values indicate the magnitude of an impact: (0) = negligible; (1) = minor; (2) = important; and (3) = very important.

	Suitability of habitat for squirrel territories (large trees with dense tree canopy cover)	Fungi (a food source) production in the needle litter	Storage effectiveness of middens	Abundance of preferred cones	Abundance of total cones	Cavities available as nest sites	Structural materials available for runways and midden sites	Cumulative impact to red squirrels (a summary)
Habitat fragmentation (stand size reduction, road construction, etc.)	-3	-1	0	-1	-1	0	0	-3
Selective harvest (thinning) of trees (windthrow is analogous to selective harvest)	-2	-2	-2	-2	-2	-2	+2	-2
Clearcutting for development (forest fires are analogous to clearcutting)	-3	-3	-3	-3	-3	-3	-3	-3
Management favoring early succession stages	-2	0	0	-2	-2	3	-1	-2
Management favoring dense, mature, or old growth spruce-fir	+3	+3	+3	+3	+3	+3	+3	+3
Management favoring dense, mature, or old growth of mixed coniferous species	+3	+3	+3	+1	+3	+3	+3	+2
Removal of snags and woody debris	0	0	-2	0	0	-2	-3	-1
Presence of tassel-eared squirrels	0	-1	0	-1	-1	0	0	-1

maintain marginal populations in marginal habitats. A rule for judging the suitability of a proposed land-use change might be that land-use change that can be accomplished while promoting trend lines like 1b3 (with strong positive slopes) or which produce conditions like line 2 in figure 6 are environmentally acceptable and can be accomplished if they are socially and economically desirable.

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Comparative Effectiveness of Pitfalls and Live-Traps in Measuring Small Mammal Community Structure¹

Robert C. Szaro,² Lee H. Simons,³ and Scott C. Belfit⁴

Abstract.—The effectiveness of pitfalls and live-traps for assessing small mammal community structure was compared in burned and unburned upland Sonoran Desert and in an elevational series of Sycamore riparian and adjacent habitats in Arizona. Although, live-traps were more effective in recapturing previously captured small mammals and usually resulted in more total captures of new individuals, neither method gave a complete assessment of small mammal community structure.

Several studies that compared various types of pitfalls and live-traps (also called box- or cage-traps) in the field (Chelkowska 1967, Boonstra and Krebs 1978, Peterson 1980, Boonstra and Rodd 1984, Mengak and Guynn 1987) found the sampling efficiency of the two methods varied considerably (Andrzejewski and Rajska 1972, Briese and Smith 1974, Cockburn et al. 1979, Williams and Braun 1983). Pitfall cone traps were more effective than live-traps in sampling small mammals, particularly shrews in southern Finland (Pankakoski 1979). In contrast, pitfalls were less effective than live-traps in capturing small-bodied mice in Durango, Mexico, although more shrews (*Notiosorex crawfordi*) were taken in pitfalls (Peterson 1976). Pitfalls of various materials, shapes, and sizes, with and without drift fences,

have been used for capturing small mammals (Howard and Brock 1961, Andrzejewski and Wroclawek 1963, Pucek 1969, Boonstra and Krebs 1978, Pankakoski 1979). This lack of standardization makes it difficult to assess the relative effectiveness of pitfalls versus live-traps in sampling small mammals by comparing data between studies. Conflicting results from these studies argue for more comparisons using controls for as many extraneous factors as possible.

Small mammals respond dramatically to many environmental factors, thus confounding attempts to assess species or community relationships. Sampling biases caused by climate and differences in activity and locomotor adaptations of various species further compound this problem. Still, trapping remains the most practical method for assessing small mammal populations (Williams and Braun 1983). Because responses to trapping methods may differ, even within the same species (Andrzejewski and Rajska 1972), diverse sampling schemes might reveal population dynamics and community structure more completely than any single method (Weiner and Smith 1972, Boonstra and Krebs 1978).

We compared the effectiveness of live-traps versus pitfalls in riparian and desert habitats in Arizona to answer the following questions: (1) Does sampling method influence estimates of species composition and abundance? (2) Are various species

captured or recaptured differentially? (3) Are individuals within a species captured differentially? (4) Does habitat structure influence the effectiveness of these methods?

Study Areas and Methods

Riparian and Adjacent Communities

The riparian and adjacent communities (referred to in general as the riparian area) were located at Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevations ranged from 1500 to 1630 m. Riparian communities sampled, from lowest to highest elevation, were sycamore (*Platanus wrightii*), sycamore/juniper (*Juniperus monosperma*), and sycamore/juniper (*J. deppeana*)/oak (*Quercus arizonica*, *Q. emoryi*, and *Q. hypoleucoides*) (Szaro 1988). Plant communities sampled adjacent to the riparian corridor, from lowest to highest elevation, were composite (*Heterotheca* spp.)/grassland (*Poa* spp.), juniper (*J. monosperma*) woodland, and oak (*Quercus emoryi*) woodland.

Six trap stations were set in each of six habitats: composite/grassland, sycamore riparian, juniper woodland, sycamore/juniper riparian, oak woodland, and sycamore/juniper/oak riparian forest (figs. 1-6) (36 stations in all). Trap stations consisted of two unbaited pitfalls (18.9 L or 5

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Figure 1.—Arizona sycamore (*Platanus wrightii*) study site, Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevation ca. 1500 m.



Figure 2.—Arizona sycamore (*Platanus wrightii*)/one-seed juniper (*Juniperus monosperma*) study site, Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevation ca. 1565 m.



Figure 3.—Arizona sycamore (*Platanus wrightii*)/alligator juniper (*J. deppeana*)/mixed oak (*Quercus arizonica*, *Q. emoryi*, and *Q. hypoleucoides*) study site, Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevation ca. 1610 m.



Figure 4.—Composite (*Heterotheca* spp.)/grassland (*Poa* spp.) study site, Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevations ca. 1510 m.



Figure 5.—One-seed juniper (*J. monosperma*) woodland study site, Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevations ranged from 1570 m.



Figure 6.—Emory oak (*Quercus emoryi*) woodland study site, Garden Canyon, Fort Huachuca Military Reservation, Arizona; elevations ca. 1590 m.

gal.; 29 cm in diameter by 36 cm deep) with a 7.6-m-long by 20-cm-high drift fence between buckets. Covers were propped 2.5-5 cm above openings mouths. Pitfalls were open from 16 April through 28 May and from 20 July through 5 September 1986 (6408 trap-nights) and were checked three times each week. Sherman live-traps (8 by 9 by 23 cm) baited with rolled oats were set around each pitfall station in an 8-trap pattern with at least 5 m between traps and pitfalls. Live-traps were set from 12 to 16 May and from 17 to 21 August 1986 (2304 trap-nights) and were checked each morning. Most live-trap captures were released after being ear-tagged. Except for some *Notiosorex*, all pitfall captures were collected. Identification of all mammals follows Hoffmeister (1986). *Thomomys* species include pure and hybrid *T. umbrinus* and *T. bottae*.

Desert Community

The desert study area was in the Tonto National Forest, Maricopa County, 30 km east of Phoenix, Arizona. The site was rocky desert dissected by sandy washes; elevations ranged from 450 to 550 m. Vegetation was typical of the Arizona upland subdivision of the Sonoran Desert biome (Brown 1982), with mesquite (*Prosopis juliflora*) along wash banks and palo verde (*Cercidium microphyllum*), bursage (*Ambrosia deltoides*), and cholla (*Opuntia acanthocarpa*) on slopes.

Two grids were established 90 m apart, each with 100 sampling stations placed in a 10 by 10 pattern with 10-m intervals between stations. Grid 1 was in mature desert and grid 2 had 50% of vegetative cover burned on 7 June 1985, immediately before the start of trapping (figs. 7-8). Interspaced between live-traps (10 by 10 by 25 cm) on each grid, but no closer than 10-m intervals, were 20 single pitfalls (37.9 L or 10 gal., 34 cm

diameter by 40 cm deep) buried to the rim with a cover propped 5-10 cm over the opening. Live-traps were

set and baited with rolled oats for two consecutive nights on 19 occasions between 10 June 1985 and 3

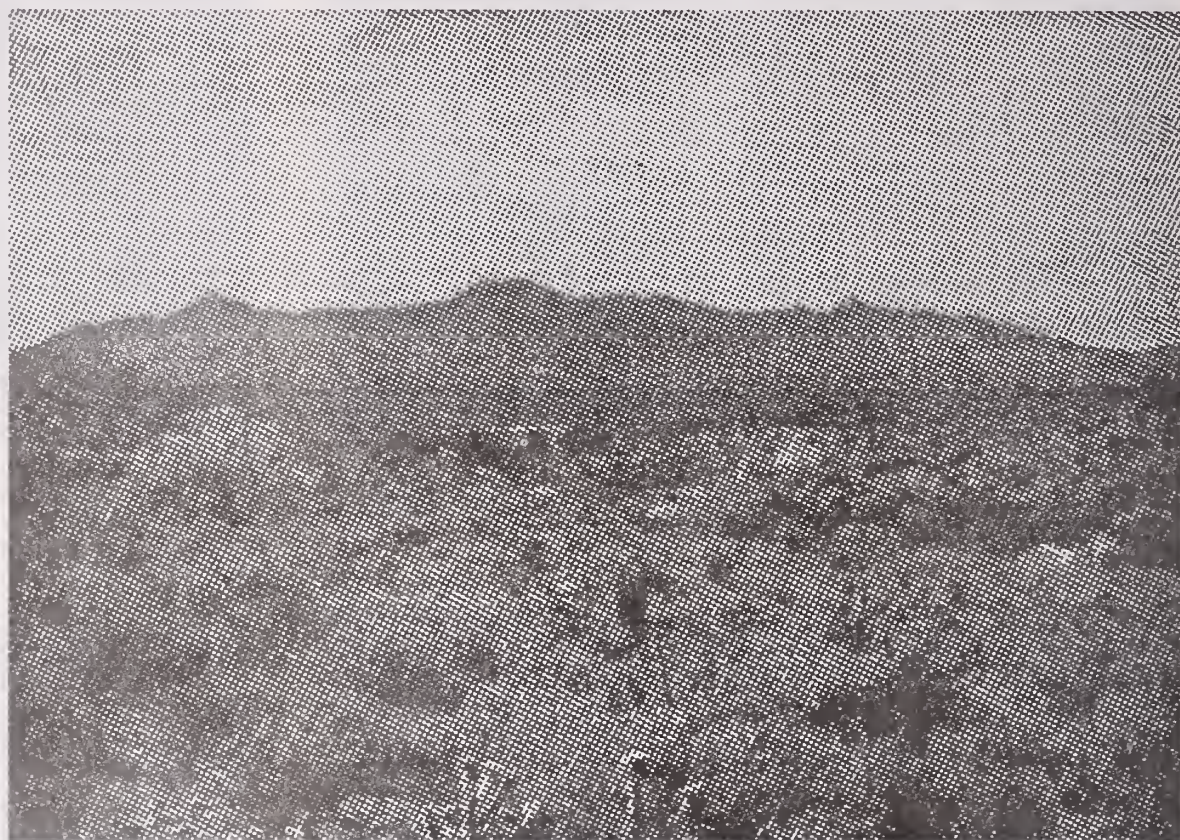


Figure 7.—Unburned desert study area, Tonto National Forest, Maricopa County, 30 km east of Phoenix, Arizona; elevation ranged from 450 to 550 m.



Figure 8.—Burned desert study area, Tonto National Forest, Maricopa County, 30 km east of Phoenix, Arizona; elevation ranged from 450 to 550 m.

August 1986—weekly in spring and early summer, biweekly from middle to late summer, and monthly in fall and winter (Simons 1986). Unbaited pitfalls were always open during live-trapping and often in between when live-trapping occurred weekly or biweekly (March-September). All captures except for casualties were marked and released. Each method was matched with an approximately equal sampling effort (about 3800 trap-nights per grid).

Results and Discussion

Species Composition and Abundance

Live-traps and pitfalls provided different estimates of species composition and relative abundance at both study areas. In the riparian area we observed no consistent pattern between trapping method and number of species captured (table 1). Live-traps caught more species in two

habitats, pitfalls, in three habitats, and in the sycamore/juniper/oak both methods captured two species. Neither method captured all species in a given habitat except in oak woodland where only two species were encountered and pitfalls captured both. However, live-trapping was significantly more successful than pitfalls in number of new captures per trap-night (chi-square, $P \leq 0.05$) in all habitats except juniper woodland, where both methods yielded equal numbers.

In the desert, live-traps caught more species than pitfalls (table 2). Moreover, significantly more new captures and total captures (chi-square, $P \leq 0.05$) occurred in live-traps than in bucket-traps in both burned and unburned plots (table 2). These results differ from those of Williams and Braun (1983) who reported that number of species and total number of captures were greater in pitfalls than in the combined catch of snap- and live-traps. They recorded six species in pitfalls

and four in snap- and live-traps. Their success with pitfalls was no doubt increased because each trap was one-third filled with water, drowning all captures. Trapping success for voles (*Clethrionomys glareolus*) was also reported to be higher in pitfalls versus live-traps but may vary with social level, age, and reproductive period (Andrzejewski and Rajska 1972, Andrzejewski and Wroclawek 1963, Chelkowska 1967).

New individuals represented only 31.5% and 26.2 % of total captures in live-traps on the burned and on the unburned plots, respectively. In contrast, 95.8% and 92.7% of all captures in pitfalls on the burned and unburned areas, respectively, represent new individuals. The lack of recaptures in pitfalls is not explained by differential mortality between methods because sampling with both methods occurred simultaneously, and most animals were marked and released. These differences may be at least partially due to increased attractiveness of live-traps with bait

Table 1.—Total number of new individuals captured in riparian and associated habitats using live-traps (384 trap-nights/habitat) and pitfalls (1068 trap-nights/habitat) during spring and late summer 1986.

Species	Composite/ grass		Sycamore		Juniper woodland		Sycamore/ juniper		Oak woodland		Sycamore/ juniper/oak		Total	
	Live- trap	Pit- fall	Live- trap	Pit- fall	Live- trap	Pit- fall	Live- trap	Pit- fall	Live- trap	Pit- fall	Live- trap	Pit- fall	Live- trap	Pit- fall
<i>Neotoma albigula</i>	1												1	
<i>Notiosorex crawfordi</i>		2		31	1	17		22		2		2	1	76
<i>Onychomys torridus</i>	8	2		1	4	4							12	7
<i>Perognathus flavus</i>	1			1									1	1
<i>Perognathus hispidus</i>	2				1								3	
<i>Perognathus pencillatus</i>			1										1	
<i>Peromyscus boylei</i>			12		1		13		13	3	12		51	3
<i>Peromyscus leucopus</i>							3				3		6	
<i>Peromyscus maniculatus</i>	5			2									5	2
<i>Reithrodontomys fulvescens</i>	4	2	5	2		1		1					9	6
<i>Reithrodontomys megalotis</i>					1								1	
<i>Sigmodon ochrognathus</i>			1										1	
<i>Sorex arizonae</i>												2		2
<i>Thomomys</i> spp.		2				1		3						6
Total captures	21	8	19	37	8	23	16	26	13	5	15	4	92	103
Species richness	6	4	4	5	5	4	2	3	1	2	2	2	12	8
Overall species richness	8		8		7		5		2		4		14	
New captures/trap-night x 100	5.07	0.75	4.95	3.46	2.08	2.15	4.17	2.43	3.38	0.47	3.90	0.37	3.99	1.61
All captures/trap-night x 100	7.26		10.38		2.10		9.84		4.92		6.00		6.75	

and with concentrated odors from previous captures (Boonstra and Krebs 1978, Daly and Behrends 1984). Our results show that pitfalls provide very different estimates of species composition and abundance than live-traps. We therefore question basic assumptions of the popular methods of population estimation that assume either equal catchability of all members in the population (Jolly 1965) or nearly complete capture and enumeration of a population (Krebs 1966, Hilborn et al. 1976).

Differential Trapping Effectiveness Between Species

In the riparian area, 80 of 81 shrews (*Notiosorex crawfordi* and *Sorex arizonae*) and all gophers (*Thomomys* spp.) were captured in pitfalls. In contrast, only 5 of 67 captures of *Peromyscus* (3 species) were in pitfalls (table 1). *Peromyscus* spp. were also recaptured most frequently (57 of 64 recaptures). Similar results were found in the Sierra Nevada where species such as shrews (*Sorex trowbridgii* and *S. monticolus*) and gophers (*Thomomys bottae*), which tend to travel in burrows or runways or along obstacles, were usually captured in pitfalls (Williams and Braun 1983). Williams and Braun (1983) reported in their first test that pitfalls were particularly poor for capturing white-footed mice (*Peromyscus*). In a subsequent test they implied these mice might be taken in pitfalls after losing their caution for strange objects. This did not happen in our study because very few *Peromyscus* were captured in pitfalls over an extended period even though live-trapping showed them to be common. More likely *Peromyscus* may easily escape pitfalls by jumping out, but more are recorded after drowning in water-filled pitfalls (Williams and Braun 1983), especially when other traps, such as snap- or live-traps, are missing.

In the desert habitat, a single shrew (*Notiosorex crawfordi*) was

caught in a pitfall whereas two species (*Dipodomys merriami* and *Peromyscus eremicus*) were caught only in live-traps. Only 1 of 181 captures (50 different individuals) of *Neotoma albigula* was in a pitfall whereas only 1 of 9 *Onychomys torridus* was not captured in a pitfall. *Onychomys* was probably unable to jump out of the buckets used in this habitat. Noted accumulations of *Neotoma* feces overnight in many pitfalls indicated these rodents had been present but left. Apparently larger species either avoid pitfalls or simply jump out of them (Cockburn et al. 1979, Williams and Braun 1983).

Differential Trapping Effectiveness Within Species

Few significant differences in weights of small mammals caught with the two methods were observed, but weights tended to be lower in pitfalls. In the riparian area, mean weights of *Reithrodontomys fulvescens* were significantly higher in live-traps (14.3 ± 0.65 (S.E.) g versus 5.1 ± 0.56 , t-test, $P < 0.001$, $N = 12$). In

the desert, weight differences between trap methods were not significant for animals less than about 20 g. However, a significant difference occurred in the mean weight of *Perognathus baileyi* in live-traps (25.7 ± 0.97 g) versus pitfalls (20.8 ± 1.61 g; t-test, $P = 0.014$). Similarly, the mean weight of *Neotoma albigula* caught in live-traps was 109.0 ± 8.93 g, whereas the single capture in a pitfall weighed 31.0 g.

Likewise in Canada and Poland, voles (*Microtus townsendii* and *Clethrionomys glareolus*) captured in pitfalls were smaller than conspecifics taken in live-traps (Andrzejewski and Rajska 1972, Boonstra and Krebs 1978). This apparent relationship between size and susceptibility to pitfalls is likely related to jumping ability which tends to increase with age. For some species, pregnant females may be more susceptible to pitfalls.

Effects of Habitat on Trapping Effectiveness

Trapping results for *Onychomys torridus* varied substantially between

Table 2.—Total number of new individuals captured in burned and unburned desert habitats using live-traps and pitfalls (3800 trap-nights/habitat/trap type).

Species	Burned		Unburned		Total	
	Live-trap	Pitfall	Live-trap	Pitfall	Live-trap	Pitfall
<i>Ammospermophilus harrisi</i>	2	1	4	1	6	1
<i>Dipodomys merriami</i>	11		3		14	
<i>Neotoma albigula</i>	11	1	38		49	1
<i>Notiosorex crawfordi</i>				1		1
<i>Onychomys torridus</i>	1	7		1	1	8
<i>Peromyscus eremicus</i>	2		3		5	
<i>Perognathus amplus</i>	91	76	85	25	176	101
<i>Perognathus baileyi</i>	18	30	21	10	39	40
Total captures	136	115	154	38	290	152
Species richness	7	5	6	5	7	6
Overall species richness		7		8		8
New captures/trap-night x 100	3.58	3.02	4.05	1.00	3.81	2.00
All captures/trap-night x 100	11.36	3.16	15.45	1.08	13.41	2.11

vegetative communities. On the desert sites, 8 of 9 captures were in pitfalls whereas in composite/grass habitat in Garden Canyon, 8 of 10 captures were in live-traps. Four captures were made with each method in the juniper woodland. Differences in trapability of *Oncychomys* may be due to different depths of pitfalls in desert (40 cm) versus riparian (36 cm) habitats.

Except for *Perognathus* spp., rodents were about equally susceptible to pitfalls relative to live-traps in both burned and unburned desert habitats. Differences in total number of individuals captured by both methods in the desert areas may be due to (1) difference in abundance of species on burned and unburned plots (Simons 1986); or (2) differences in activity patterns related to the drastic difference in shrub cover. *Perognathus* spp. typically prefer brush or "cover" microhabitats (Price 1978) and raised pitfall covers may have attracted these mice more on the burned area where natural cover was scarce than on the unburned area where natural cover was dense (Simons 1986). Whatever the cause, the results are similar to those found in desert-shrub and mesquite-grassland habitats in Durango, Mexico, where significantly more small-bodied mammals were captured with live-traps than with pitfalls (5.4 L tin can pitfalls with a depth of 25.4 cm) (Peterson 1980). Possibly a greater number of captures (i.e., sample size) may be needed to fully reveal the impact of habitat on trapping methodology.

Conclusions

Neither method alone was able to fully assess small mammal communities in the desert-scrub and riparian communities we investigated. We recommend the use of both methods, particularly when it is important to include species such as shrews that are not easily caught in live-traps in investigations of small mammal com-

munity structure and habitat relationships.

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The Role of Habitat Structure in Organizing Small Mammal Populations and Communities¹

Gregory H. Adler²

Environmental heterogeneity has maintained a position of prominence in theoretical population and community ecology (reviewed by Levin 1976, Wiens 1976, and Wiens et al. 1986). Heterogeneity allows organisms to select different habitats, which subsequently can have profound consequences for the organization of populations and communities. Environmental heterogeneity can be studied, both theoretically and empirically, at different scales. Conclusions based on the study of habitat structure may differ widely depending upon the scale of structure examined. The scale of environmental subdivision can be viewed as occurring along various continua, e.g., from the area occupied by a single individual to a biogeographic or continental area (Wiens et al. 1986), or from microhabitat to macrohabitat.

In this paper, I concentrate on the microhabitat to macrohabitat scale. I define microhabitat as physical habitat characteristics likely to vary over the home range of a single individual (e.g., the number of herbaceous stems within a circumscribed area) and macrohabitat as the major habi-

tat type where an entire population may be found (e.g., grassy field or deciduous woodland in the case of small mammals). Microhabitat structure therefore can vary substantially within a single macrohabitat.

I summarize results from a series of long-term studies on the role of habitat structure in organizing small mammal populations and communities that I conducted in eastern Massachusetts. These studies were designed to examine (1) habitat associations and habitat selection and the roles of intra- and interspecific interactions in affecting habitat utilization, and (2) the influence of habitat structure on density and demography. In these studies, I focus primarily on microhabitat structure, and I develop a conceptual scheme which shows how microhabitat and macrohabitat structure organize small mammal populations and communities.

STUDY SITES AND GENERAL METHODS

Study Sites

The long-term studies were conducted at three sites in eastern Massachusetts: Broadmoor/Little Pond Audubon Sanctuary, South Natick; Great Island, near West Yarmouth; and the University of Massachusetts Nantucket Field Station, Nantucket. Sampling areas within each study

Abstract.—Microhabitat structure influences population density more than other demographic variables such as age and sex composition. Microhabitat heterogeneity, or quantitative variation in microhabitat structure, apparently has little influence on phenomena such as population stability. Scale mediates effects of habitat structure and heterogeneity on population and community organization. I suggest that microhabitat structure influences density more than other aspects of demography, whereas macrohabitat structure and heterogeneity are more important in influencing population stability, demography, and community structure.

site were confined to a 300-ha area and were exposed to the same climate and the same predators, competitors, and parasites.

Broadmoor consists of a mosaic of grassy fields separated by mixed deciduous-coniferous woodland. Sampling at Broadmoor was confined to the fields, which were dominated by the grasses *Agropyron repens* and *Poa pratensis*. Other herbaceous and woody plants, including goldenrod (*Solidago* spp.), milkweed (*Asclepias syriaca*), poison ivy (*Rhus radicans*), and several species of deciduous tree saplings, were much less prevalent.

Great Island is a 240-ha island connected to mainland Cape Cod by a causeway. The island is dominated by deciduous and coniferous woodland but has structurally simpler habitat along the shore. This shoreline habitat consists primarily of beach grass (*Ammophila breviligulata*), with patches of poison ivy, Virginia creeper (*Parthenocissus quinquefolia*), bayberry (*Myrica pensylvanica*), rose (*Rosa carolina*), and juniper (*Juniperus virginiana*).

Nantucket Island (ca. 12,300 ha and lying approximately 30 km off the coast of Cape Cod) has large areas of low, dense woody growth (heath) where small mammals were sampled. Heath at the study site was composed primarily of rose and bayberry, with patches of goldenrod and other herbaceous plants and grasses interspersed within the brush. Scattered juniper trees also were present.

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Sampling Procedures

I sampled small mammals at each study site by monthly live-trapping with Longworth live-traps for approximately 4 to 5 years. At each study site, I monitored two 0.4-ha grids located in grassy or brushy habitat. One grid served as a control in which all small mammals were individually marked by ear-tags (rodents) or toe-clips (insectivores). The other grid, located 30.4 m from the control and situated in contiguous habitat, served as an experimental grid from which all small mammals were removed permanently upon first capture (Adler 1985). All small mammals captured on this grid after the initial removal period were considered colonists. I also sampled small mammals on 4 nearby trapping plots which also were located in similar macrohabitat but covered a range of microhabitats. Each plot consisted of two parallel traplines located 30.4 m apart. Each trapline was 15 stations long at Broadmoor (except on one plot where both traplines were 12 stations long) and on Nantucket and 20 stations long on Great Island. These plots were trapped on a rotation basis (Adler 1987). On Great Island, an additional 4 control grids were monitored monthly from April through September for five years (Adler and Wilson 1987). These grids were not confined to structurally simple macrohabitats but ranged from grassland to mature woodland habitats.

Grid 1 was located at the edge of a stand of pitch pine. (*Pinus rigida*), white oak (*Quercus alba*), and black oak (*Q. velutina*). Dense brushy understory covering a large portion of the grid consisted of bayberry, huckleberry (*Gaylussacia baccata*), and inkberry holly (*Ilex glabra*). Low-lying areas of the grid were damp and harbored large cranberry (*Vaccinium macrocarpon*) and sundew (*Drosera* spp.). Very little herbaceous vegetation was present. Grid 2 also was located at the edge of a pitch pine,

white oak, and black oak woodland but was more elevated and consequently drier. A dense brushy understory consisted of bayberry, poison ivy, and common greenbrier (*Smilax rotundifolia*). Grass was present in the

brushy, treeless portions of the grid. Grid 3 was located within a white oak and black oak woodland. A dense shrub cover of blueberry, bearberry (*Arctostaphylos uva-ursi*), common greenbrier, and bullbrier

Table 1.—Description of the habitat variables measured at each trap station. All variables measured as proportions was arcsin square root transformed.

Name	Description
WOOD	Density of woody stems within a 1-m ² circle at ground level.
HERB	Number of herbaceous stems (excluding grasses and sedges) within a 1-m ² circle at ground level.
WDSPEC	Number of woody species within a 1-m ² circle at ground level.
HBSPEC	Number of herbaceous species (excluding grasses and sedges) within a 1-m ² circle at ground level.
HB50	Number of herbaceous stems (excluding grasses and sedges) within a 1-m ² circle at 50 cm above ground level.
HB100	Number of herbaceous stems (excluding grasses and sedges) within a 1-m ² circle at 1 m above ground level.
VHBDEN	Mean of HERB, HB50, and HB100.
WD50	Number of woody stems within a 1-m ² circle at 50 cm above ground level.
WD100	Number of woody stems within a 1-m ² circle at 1 m above ground level.
VWDEN	Mean of WOOD, WD50, and WD100.
OVER	Number of overstory species within a 15-m ² circle.
UNDER	Number of shrub level species within a 15-m ² circle.
FORB	Number of forb species within a 15-m ² circle.
GRASPEC	Number of grass and sedge species within a 15-m ² circle.
GRNDSPEC	Number of woody ground-dwelling vine species within a 15-m ² circle.
SPECIES	Total number of angiosperm and gymnosperm species within a 15-m ² circle.
TPSHRUB	Transformed proportion of a 15-m ² circle dominated by woody shrub-level vegetation.
TPHERB	Transformed proportion of a 15-m ² circle dominated by herbaceous vegetation (excluding grasses and sedges).
TPGRND	Transformed proportion of 15-m ² circle dominated by woody ground-dwelling vines.
TPGRASS	Transformed proportion of 15-m ² circle dominated by grasses and sedges.
TPVEG	Transformed proportion of a 15-m ² circle covered by vegetation.
HBGRND	An index of herbaceous ground cover (excluding grasses and sedges), calculated as HERB-HB50.
WDGRND	An index of woody ground cover calculated as WOOD-WD50.
TPCANOPY	Transformed proportion of a canopy cover measured only on the five Great Island control grids.
TPGREEN	Transformed proportion of evergreen canopy cover, measured only on the five Great Island control grids.

greenbrier (*S. bona-nox*) was present, along with bracken fern (*Pteridium aquilinum*). Grid 4 was located on Pine Island, a 7-ha islet 37 m from Great Island and connected to the latter by a narrow sandy spit. White oak and black oak formed a canopy over much of the grid, and a dense woody understory of bayberry and other shrubs also was present. Dense beach grass was present in the treeless portions of the grid. Grid 5 was

the companion control for the experimental grid and was located in dense beach grass containing scattered patches of bayberry, juniper, and poison ivy.

I sampled vegetation structure at every trap station on all grids and plots by measuring 23 habitat variables related to plant structure and species richness (table 1). Two additional habitat variables describing canopy structure were included in

the analysis on Great Island control grids (table 1). Measurement procedures were given by Adler (1985) and Adler and Wilson (1987).

Data Analysis

I relied extensively upon principal components analysis (PCA) and discriminant function analysis (DFA) in order to uncover the structure of complex and temporally variable small mammal populations and their relationships to habitat structure. Specifically, my aims were to (1) reduce the number of habitat dimensions, (2) derive a quantitative measure of habitat heterogeneity, (3) quantify patterns of habitat utilization, (4) combine covarying demographic traits into single variables, and (5) derive indices of demographic variability.

In these studies, I recognized two related descriptors of microhabitat structure. I defined a microhabitat structure-diversity variable or gradient as a characteristic that described the physical structure of the microhabitat and that varied in magnitude along a continuum. I defined microhabitat heterogeneity as a quantitative measure of horizontal variation in microhabitat characteristics (August 1983, Adler 1987).

I subjected the habitat data measured at each trap station to PCA to reduce the number of habitat variables. At each site, I conducted two PCAs of the 23 variables, one with control and experimental grids combined and one with the 4 trapping plots combined. I also conducted a PCA of 24 habitat variables for all five control grids on Great Island combined. HB100 was eliminated from this analysis because only one nonzero value was recorded on the five grids.

Each principal component (PC) with an eigenvalue greater than 1.0 was retained for further analysis as a new habitat variable. Principal components derived from PCAs of grid

Table 2.—Summary of the sampling design and statistical approach employed in this study.

Sampling area	Topic	Methods
Control grid	Habitat associations.	Multiple linear regression of numbers of captures at a trap station on microhabitat variables derived from PCA.
	Temporal dynamics of habitat use.	DFA to derive a quantitative measure of seasonal habitat use (the distinction between favorable and unfavorable microhabitats, or habitat discrimination). Regression of discrimination values on population densities to determine the relationship between microhabitat use and intra- and interspecific population densities.
Experimental grid	Habitat selection.	Multiple linear regression of numbers of captures at a trap station (in a perturbed area) on microhabitat variables derived from PCA, compared with control grid.
Trapping plots	Relationship between demography and microhabitat structure within a macrohabitat.	Regression (and residual analysis) of demographic variables on plot means of microhabitat gradients and heterogeneity.
Additional control grids (4 at Great Island)	Relationship between demography and microhabitat structure of a habitat generalist across macrohabitat boundaries.	Regression (and residual analysis) of demographic variables on grid means of microhabitat gradients and heterogeneity.

and plot data were quite similar within each site, based upon factor loadings on the original habitat variables (Adler 1985, 1987). At Broadmoor, five PCs were retained for analysis from both grid and plot data, whereas six were retained from analysis of grid data; four PCs were interpreted similarly in both data sets. PCAs of Nantucket grid and plot data both yielded seven retainable PCs, three of which could be interpreted similarly between the two data sets. The PCA of habitat data from the five control grids on Great Island yielded seven PCs.

I computed a microhabitat heterogeneity index for each of the four trapping plots at the three study sites and for each of the five control grids on Great Island (Adler 1987, Adler and Wilson 1987). This index was based on the supposition that the standard deviation of the within-plot or within-grid mean vector of a PC described the variability of a microhabitat gradient on a given plot or grid. Since each successive PC contributed less to the total variance in

habitat data, I adjusted for each PC's contribution to the total variance by multiplying the factor scores by the square root of that PC's eigenvalue.

I examined capture data in relation to habitat structure at both the level of individual trap stations (habitat association and selection) and at the level of a grid or plot (demography). I used multiple linear regression and residuals analysis to relate these small mammal (dependent) variables to habitat (independent) variables. More complete descriptions of analytical techniques are given in each section below, and a brief outline of the sampling design is given in table 2.

SPECIES COMPOSITION

I recorded 9,170 captures of 10 small mammal species in 42,773 trapnights at the 3 study sites (table 3). Each study site generally had an abundant herbivore (*Microtus pennsylvanicus*), an abundant granivore (*Peromyscus leucopus*, except at Broadmoor where

it was rare in the grassland trapping areas), a common insectivore (*Blarina brevicauda* or *Sorex cinereus*), and any of several rarer granivores, omnivores, or insectivores.

HABITAT STRUCTURE AND POPULATION STATISTICS

Habitat Associations and Selection

Study Purpose

I examined both small mammal microhabitat associations and selection at all three study sites (Adler 1985). Density-dependent effects of conspecifics and other species may restrict access to certain habitat types, thereby resulting in different patterns of habitat utilization. I therefore reserved the term habitat selection for situations where individuals had more or less unrestricted access to a variety of habitat types.

Table 3.—Trapping effort and numbers of captures of small mammals at three study sites in eastern Massachusetts. Species designations are MP (*Microtus pennsylvanicus*), PL (*Peromyscus leucopus*), BB (*Blarina brevicauda*), SC (*Sorex cinereus*), ZH (*Zapus hudsonius*), RN (*Rattus norvegicus*), SA (*Scalopus aquaticus*), TS (*Tamias striatus*), CG (*Clethrionomys gapperi*), and CC (*Condylura cristata*).

Site	Trap periods	Trap-nights	MP	PL	BB	SC	ZH	RN	SA	TS	CG	CC	TOTAL
Broadmoor													
Control	32	3332	416	1	76	7	6	0	0	0	0	0	507
Exptl.	32	3136	225	11	61	5	23	0	0	2	0	1	327
Plots	32	1824	212	19	48	7	8	1	0	0	0	0	295
Great Island													
Ctl (1)	43	4157	86	400	0	22	18	0	0	15	7	0	548
Ctl (2)	31	2940	146	359	25	12	7	0	0	39	0	0	588
Ctl (3)	31	2989	12	358	13	10	0	0	0	71	0	0	464
Ctl (4)	30	2934	551	404	0	41	0	0	0	0	0	0	996
Ctl (5)	43	4193	603	349	11	61	21	0	0	3	0	0	1048
Exptl.	35	3381	219	111	15	74	18	0	0	1	0	0	438
Plots	35	2686	336	221	3	54	12	0	0	0	0	0	626
Nantucket													
Control	35	5782	1364	255	83	0	3	2	2	0	0	0	1709
Exptl.	35	3621	420	270	75	2	0	3	0	0	0	0	770
Plots	35	1798	400	420	28	0	0	6	0	0	0	0	854
TOTAL	449	42773	4990	3178	438	295	116	12	2	131	7	1	9170

Analytical Approach

I defined an association as a statistical relationship between the numbers of captures of a species at trap stations and a quantitative measure of microhabitat structure. To determine these relationships, I regressed the total number of captures of a species at each control grid trap station on factor scores of each PC. The experimental grid represented an area where densities were continually being reduced and vacant microhabitats were more often available to colonizing individuals.

To determine differences in microhabitat associations between control and experimental grids, I included a dummy variable coding for grid (control or experimental) and habitat variable \times grid interaction terms (Adler 1985).

Inferences

Most small mammals (8 of 11 populations examined) demonstrated affinities for specific microhabitat types on either control or experimental grids (table 4). These affinities generally were consistent with other published reports of habitat associations of these species. For instance, *P. leucopus* generally were associated positively with woody microhabitats or negatively associated with herbaceous microhabitats. *M. pennsylvanicus* generally showed the opposite associations. Microhabitats selected by small mammals, as determined from capture data on experimental removal grids, sometimes differed from associations determined from capture data on the adjacent control grids (table 4). Differences in habitat selection and association were attrib-

utable to opportunistic responses of small mammals to between-grid differences in microhabitat structure and to differences in the level of intraspecific interactions brought about through density reductions on the experimental grids (Adler 1985).

Temporal Patterns of Habitat Use

Study Purpose

I examined temporal patterns of microhabitat use by *M. pennsylvanicus* at the three study sites and by *P. leucopus* on Great Island and Nantucket.

Analytical Approach

Monthly trapping periods were grouped into winter (Dec.-Feb.), spring (Mar.-May), summer (Jun.-Aug.), and fall (Sep.-Nov.) seasons each year. I divided trap stations on control grids into favorable and unfavorable microhabitats each season depending upon whether the total number of captures in a season was above (favorable) or below (unfavorable) the seasonal mean (Van Horne 1982; Adler 1985). I then used a two-group DFA, with favorable and unfavorable trap stations defining the two groups, to develop a discrimination index of habitat use (Rice et al. 1983; Adler 1985). This index was the percentage of trap stations classified correctly as either favorable or unfavorable. High discrimination values indicated a sharp distinction between favorable and unfavorable microhabitats; low values indicated little difference between favorable and unfavorable areas.

To determine the importance of intra- and interspecific population densities on temporal patterns of habitat discrimination by *P. leucopus* and *M. pennsylvanicus*, I regressed the seasonal discrimination values on the mean seasonal densities of each of the major small mammal species present at each study site.

Table 4.—Habitat associations of small mammals in eastern Massachusetts determined from regressions of numbers of captures at trap stations on habitat variables derived from principal components analysis. The direction of the regression slope is given by + or - and the strength of the relationship is given by the number of signs (1, $P < 0.05$; 2, $P < 0.01$; 3, $P < 0.001$). Species designations are as in table 3.

Site and Species	Description of habitat variable	Control grid	Experimental grid
Broadmoor			
BB	All variables	NS	NS
MP	Herbaceous density and height	+++	---
	Shrubby vegetation	-	NS
	Ground-level herbaceous density	-	+
ZH	Herbaceous density and height	NS	+
Great Island			
SC	All variables	NS	NS
BB	Vertical woody vegetation density	+	+
PL	Total vegetation cover, primarily herbaceous	NS	---
MP	Habitat complexity	---	NS
	Habitat structure, reflecting increasing herbaceousness and decreasing woodiness	+	NS
	Ground-level woody vine density		
ZH	All variables	NS	NS
Nantucket			
BB	Herbaceous species richness	+	NS
PL	Number of overstory trees	+	NS
	Vertical vegetation structure	NS	+
MP	Herb species richness	-	NS

Inferences

In the case of *M. pennsylvanicus*, density and discrimination were negatively related at Broadmoor and positively related on Great Island. The unexpected positive relationship on Great Island could be explained by the distribution of captures over the grid; 17 capture stations had less than two captures during the entire study and were in a sparsely vegetated area. As density increased, the remaining 32 trap stations became increasingly utilized. The distinction between favorable and unfavorable microhabitats increasingly became a distinction between unoccupied, sparsely vegetated stations and occupied, densely vegetated stations.

On Nantucket, discrimination followed a pattern similar to density but was not linearly related to the latter. For *P. leucopus* on both Great Island and Nantucket, habitat discrimination was related negatively to density (fig. 1), indicating that the distinction between favorable and unfavorable microhabitats decreased with increasing density. Densities of other species were not related to temporal variation in habitat use (Adler 1985).

Therefore, intraspecific competition appeared to be more important than interspecific interactions in determining microhabitat use by the species I examined. As intraspecific density increased, the range of microhabitat types utilized also increased, as predicted by early theories of habitat selection (e.g., Svardson 1949).

Microhabitat Structure and Demography

Study Purpose

I examined the relationship between demography of *M. pennsylvanicus* and microhabitat structure from data collected on the four trapping plots at each study site (Adler 1987).

Analytical Approach

I calculated density (\log_{10} number per 100 trapnights), sex composition (proportion males, arcsin square root transformed), age structure (proportion of adults captured during sampling periods from April through September, arcsin square root transformed), and breeding intensity (proportion of adults in breeding condition captured in sampling periods from April through September, arcsin square root transformed) each trapping period.

I also computed variability measures for each of these demographic

variables as squared distances from plot means. I divided the estimates for density variability on each plot by the mean density of the respective plot in order to adjust for population size.

I regressed the estimates for each of the eight demographic variables separately on plot means for each microhabitat variable derived from PCA and the index of heterogeneity. I then regressed the unstandardized residuals from each of these regressions separately on each habitat PC and the heterogeneity index to search for nonlinearities and missing variables (Framstad et al. 1985).

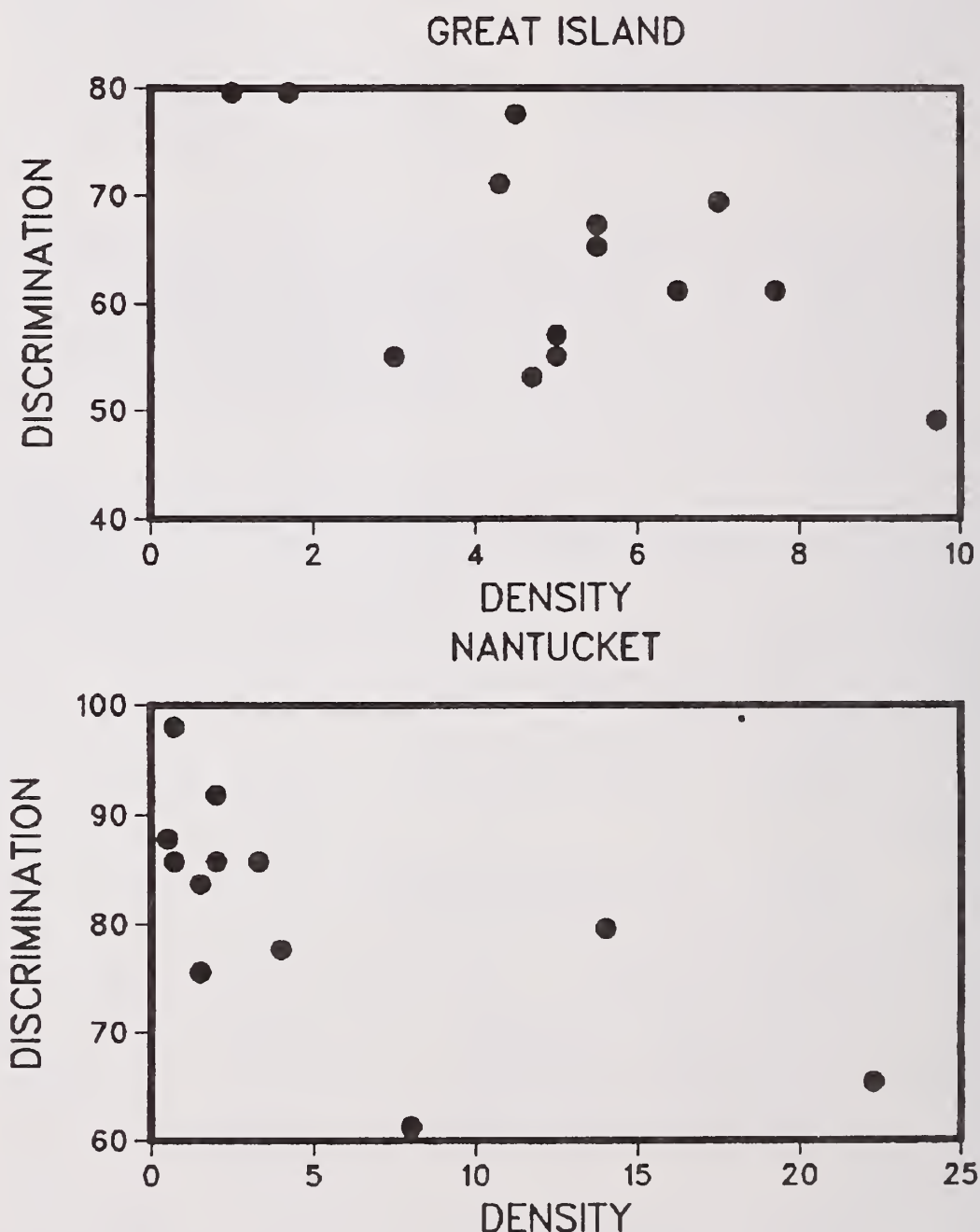


Figure 1.—Relationships between seasonal habitat discrimination and population density in *Peromyscus leucopus* at two study sites in eastern Massachusetts.

Inferences

Densities of *M. pennsylvanicus* and *P. leucopus* were ordered linearly along microhabitat gradients (Adler 1987), consistent with patterns of microhabitat associations and selection in these two species (table 5). In general, *M. pennsylvanicus* densities were higher on plots with more herbaceous and grassy cover or less woody cover. Nantucket was exceptional, however, with *M. pennsylvanicus* densities increasing along gradients of increasing woody growth and shrub species richness. I captured large numbers of this vole in dense heath with little or no herbaceous vegetation.

Peromyscus leucopus densities on Great Island could not be related to microhabitat structure, probably because of the generalist nature of this mouse relative to the breadth of microhabitats sampled. Indeed, when sampling areas included other microhabitats, density could be related to overall microhabitat structure (see below). *P. leucopus* densities on Nantucket increased with increasing shrub species richness (table 5). Densities of both species were more vari-

able in poorer habitats. Microhabitat structure was a poor predictor of other aspects of demography such as age and sex composition. However, variability in demographic structure often was greater in low-density habitats. While some of the variability in density and demography may have been due to statistical dependence on population size (i.e., greater sampling error at small population sizes), biological effects (e.g., response to environmental fluctuations) also must have been important. More favorable microhabitats should have maintained a more stable composition over time due to greater intraspecific interactions, whereas poorer microhabitats should have contained a more unstable assemblage of predominantly transient and subordinate individuals due to spillover during periods of high density (Adler 1987). In contrast to the importance of microhabitat gradients, the quantitative measure of microhabitat heterogeneity generally was unrelated to demographic phenomena. In only one case did microhabitat heterogeneity explain variation in demography better than any structure-diversity variable.

Macrohabitat Structure and Demography

Study Purpose

I further examined the relationship between demography of *P. leucopus* and microhabitat structure across macrohabitats. *P. leucopus* is a habitat generalist which occurs in habitats ranging from grassland to mature deciduous and coniferous forests in southeastern Massachusetts.

Analytical Approach

For this purpose, data from the five control grids on Great Island were analyzed (Adler and Wilson 1987). Monthly trapping data were analyzed with respect to 10 demographic variables. Grid means of density (\log_{10} minimum number known alive), adult male body mass, and observed range length (ORL, the maximum linear distance between capture points of an individual, Stickel 1954) were compared using Tukey's multiple comparisons test. Mean male and female ORLs were compared on each grid using t-tests.

Contingency table analysis was used to compare age structure (proportion adult), adult survival (standardized 14-day rates), sex composition (proportion of mice tagged that were males), adult residence rates (proportions of adults captured in at least two trapping periods), overwinter residence (proportions of mice present during Sep. and surviving to the subsequent Apr.), the proportions of adults that were reproductively active, and the proportions of young mice (mice with some grey pelage remaining) that were reproductively active. These 10 variables were examined for intersex differences within a grid (except sex composition) and for intergrid differences.

To examine temporal dynamics of demography, monthly trapping data were grouped into early summer

Table 5.—Relationships between density of *Peromyscus leucopus* (PL) and *Microtus pennsylvanicus* (MP) and microhabitat variables (derived from principal components analysis) at three study sites in eastern Massachusetts. Signs of correlation are as indicated in table 4.

Site	Species	Habitat variable	Correlation
Broadmoor	MP	Decreasing vertical woody stem densities and shrub cover.	+
Great Island	PL	All gradients.	NS
	MP	Increasing woody and herbaceous stem densities, cover and species richness; decreasing grassiness	---
		Increasing woody ground vine species richness and cover.	---
Nantucket		Increasing total vegetation cover	++
		decreasing overstory species richness.	
	PL	Increasing shrub species richness.	+
	MP	Increasing herbaceous growth; decreasing woody growth.	-
		Increasing plant species richness.	+
		Increasing shrub species richness.	+

(Apr.-Jun.) and late summer (Jul.-Sep.) seasons. The following demographic variables were estimated on each grid during each season: density (mean \log_{10} minimum number known alive), proportions of males and of females that were adults, proportion of males, mean adult male body mass, proportions of adult males and of adult females breeding, and survival rates of adult males and of adult females (weighted mean 14-day rates). Variables expressed as proportions were arcsin square root transformed.

Many rodent population parameters are known to covary (e.g., Schaffer and Tamarin 1973). Accordingly, a PCA of the eight variables was executed in order to include covarying parameters as single demographic variables; four PCs with eigenvalues greater than 1.0 were retained for further analysis.

These PCs were correlated with (1) density and adult survival, (2) adult female breeding activity, (3) adult male breeding activity, and (4) the proportion of males. Variability indices of each of these PCs were calculated each season for each grid as squared distances from grid means (Adler and Wilson 1987). A measure of overall demographic variability was calculated for each grid each season as squared distances of the factor scores from the mean factor score, summed over the four PCs.

Factor scores within each PC were multiplied by the square root of that PC's eigenvalue in order to account for the unequal contributions to overall variance of each PC (Adler and Wilson 1987). This method allowed variables with different scales of measurement to be included together without further scaling or weighting. Seasonal estimates of each of the PCA-derived demographic variables and their variability estimates were regressed separately on each of the PCA-derived microhabitat variables and the index of heterogeneity.

Inferences

Statistical tests which were significant at $P < 0.05$ are qualitatively summarized in table 6. Grid means of the first three demographic PCs revealed three demographic groups. Grids 1 and 5 were located farthest from any adjacent grid in three-dimensional space, whereas grids 2, 3, and 4 were clustered more tightly together with respect to demographic structure (table 7). Grid 1 was characterized by low density and survival, a low proportion of females, low breeding intensity, and high demographic variability. Grid 5 was characterized by low density and survival, a high proportion of females, moderate breeding intensity, and high demographic variability. Grids 2, 3, and 4 were characterized by high density and survival, low to moderate proportion of females, moderate to high breeding intensity, and low demographic variability. Two low-density groups (represented by grid 1 and grid 5) and one high-density group (represented by grids 1, 2, and 3) therefore

were evident. The low-density groups were more variable in terms of each of the demographic PCs and in overall demographic structure. In general, density, survival, and breeding activity increased along gradients of increasing woodiness or decreasing herbaceousness, whereas demographic variability decreased along these gradients (table 8).

SYNTHESIS

I found microhabitat structure to be a potentially important force in organizing small mammal populations, particularly in relation to associations and densities. Small mammals generally were associated with particular microhabitats, as revealed by analysis of single trap stations. However, associations often differed between control and experimental grids. I suggest that the small mammals I studied selected specific microhabitats and were opportunistic in their responses to habitat not occupied by other individuals (as on the

Table 6.—Summary of differences in demography of *Peromyscus leucopus* on Great Island, determined from monthly trapping data on five grids.

Variable	Comment
Density	Grids 1 and 5 had lower densities than grids 2, 3, and 4.
Adult male body mass	No differences.
Observed range length	Males had a greater ORL than females on grid 2.
Proportion male	Grids 2, 3, and 4 had a higher proportion of adult males. Grid 3 had a higher proportion of adult males than females.
Adult breeding activity	Grids 1 and 5 had a lower proportion of males breeding than grids 2, 3, and 4. Grid 1 had a lower proportion of females breeding than did the other grids. A higher proportion of females was breeding on grids 1, 3, and 4 than were males.
Young breeding activity	No differences.
Adult residence	Grids 1 and 5 had lower residence rates of adult males than grids 2, 3, and 4.
Overwinter residence	No differences.
Adult survival	Males on grids 1 and 5 had poorer survival rates than on grids 2, 3, and 4.

experimental grids). Since most small mammals that I studied were microhabitat selectors, microhabitat structure therefore was a crucial determinant of local community composition. Furthermore, microhabitat structure also should have affected temporal variability of community structure since populations in low-density areas were more variable.

Affinities of each small mammal species for particular microhabitats resulted in density-habitat relationships when averaged over a larger sampling area (grids or plots). Thus, small mammal densities generally could be related to microhabitat structure. Survival and breeding activity, which generally covary with density, also could be related to microhabitat structure when sampling areas spanned macrohabitat boundaries. The importance of microhabitat structure in affecting other demo-

graphic characteristics such as sex composition and age structure was not as pronounced. Gradients of microhabitat structure can be envisioned as comprising an environmental suitability gradient, with the endpoints being uninhabitable and optimal (where individual fitness is highest). Demographic characteristics then vary along this gradient of suitability and along other gradients. The gradient of suitability is composed of factors related not only to habitat structure but also to food resources and release from predation, competition, and parasitism. Density alone may not be a strong correlate of suitability (Van Horne 1983), but density in concert with survival and breeding activity should increase along the gradient of suitability. By contrast, demographic variability should decrease along this gradient. Several habitat types may represent

similar conditions of environmental suitability, particularly for habitat generalists such as *Peromyscus leucopus*. Therefore, it may be difficult to relate demography to microhabitat structure because similar demographic structure may be found in different habitats (Adler and Wilson 1987).

Quantitative measures of habitat heterogeneity generally were unrelated to demographic variables, in contrast to the mass of theory predicting that heterogeneity promotes population stability (e.g., den Boer 1968, Levins 1969, Smith 1972, Maynard Smith 1974, Steele 1974, Tanner 1975, Stenseth 1977, 1980, Lomnicki 1978, 1980, de Jong 1979, Hassell 1980). The contrast between my results and theoretical predictions may be reconciled by introducing scale. My measures of heterogeneity were at the microhabitat level, whereas many models have implied macrohabitat heterogeneity so that organisms may disperse into a patch and establish a resident population (e.g., Levins 1969). Increasing the number of such patches increases the spatial heterogeneity of an area, which then promotes population stability. I suggest that microhabitat structure will affect density more than it will other demographic characteristics, whereas macrohabitat structure and heterogeneity will be more important in stabilizing populations and in influencing demographic structure (e.g., sex composition and age structure).

My conclusions concerning the importance of habitat structure in organizing small mammal populations and communities can be shown schematically (fig. 2). According to this scheme, microhabitat structure primarily affects habitat selection, density, and density variability (since density generally is related inversely to variability). Macrohabitat structure primarily affects population stability (stability being enhanced by macrohabitat heterogeneity) and demographic structure. Habitat se-

Table 7.—Distances between grid means of the first three principal components derived from an analysis of demographic data of *Peromyscus leucopus*.

Grid	2	3	4	5
1	1.14	1.38	1.36	1.09
2	—	0.46	0.45	1.00
3	—	—	0.22	1.26
4	—	—	—	1.07

Table 8.—Relationships between *Peromyscus leucopus* demographic variables and habitat variables derived from PCA on Great Island. Signs of relationships are as indicated in table 4.

Demographic variables	Habitat variables	Correlation
Density and survival	Herbaceous ground-level vegetation	-
Adult male breeding activity	Herbaceous ground-level vegetation	-
	Woody ground vine species richness	+
Variability of density and survival	Herbaceous cover and species richness	+
Variability of male breeding activity	Herbaceous ground-level vegetation	---
Variability in sex composition	Woody vegetation density and richness	---
	Herbaceous cover and species richness	+++
	Canopy cover	-

lection and demography then determine local community composition and variability, respectively. While habitat structure ultimately determines community composition, it does so at the population or individual level. Therefore, I added no direct links between habitat structure and the community variables.

Additional links may be added; factors such as random events, competition, predation, parasitism, and infection manifest their effects at various levels. For instance, a predator may selectively feed on a particular species, thereby depressing its density and affecting community composition and structure. Competition between species also may affect species densities in certain small mammal communities. The structurally simple habitats that I have studied generally contain an abundant herbivore, an abundant granivore, a common insectivore, and any of several rarer omnivores. These poorly diversified communities are quite different from other systems such as deserts or tropical forests where communities are comprised of regularly structured guilds containing several species. Competition, which apparently is important in structuring communities in other areas (e.g., Brown and Bowers 1984), should not be very important. The opportunity for competition between guilds would be expected to be quite low. The occurrence of several easily studied genera with interesting life-history traits (e.g., *Microtus*, *Peromyscus*, and *Tamias*) made these sites ideal for population-level studies, but because of poorly diversified guilds or even guild singularity (only one species per guild) at my study sites, these same areas were far less suitable for community-level studies.

Habitats with which different species of small mammals are associated are well known, but the effects of relevant scales of habitat structure are only now becoming apparent. I suggest that future studies shift from repetitious descriptions of habitats

with which well-studied species associate to innovative experimental approaches that test hypothesized effects of habitat structure on population and community organization and that identify relevant scales of such structure.

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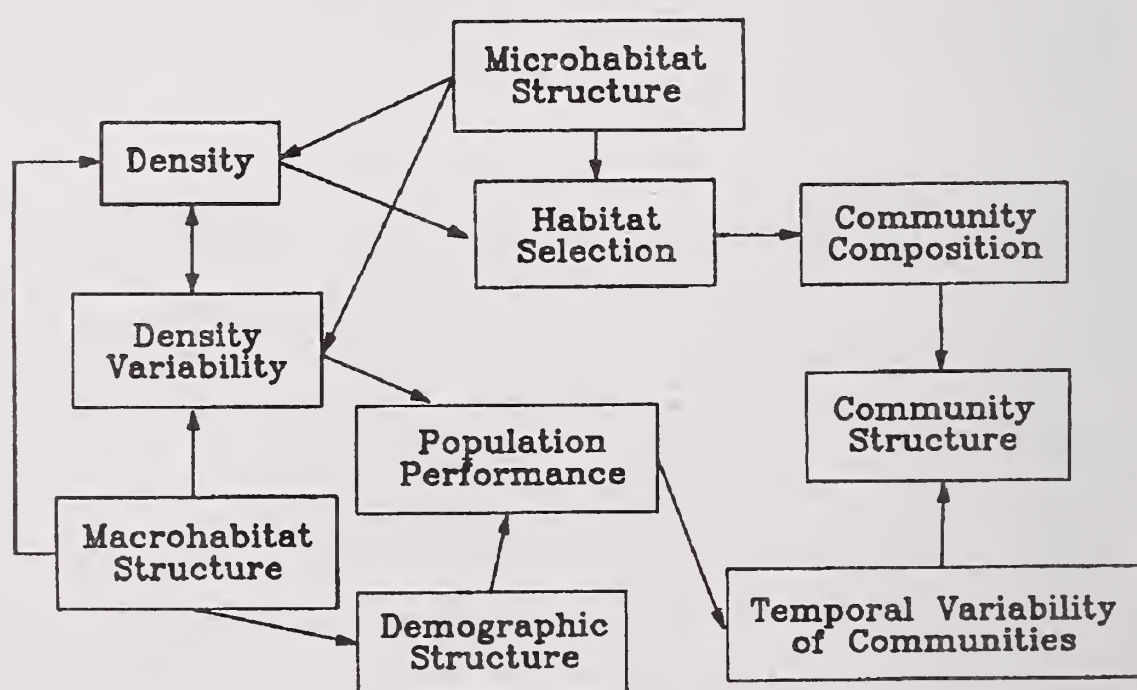


Figure 2.—Conceptual scheme showing the effects of habitat structure on population and community processes.

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Microhabitat as a Template for the Organization of a Desert Rodent Community¹

Michael A. Bowers² and Christine A. Flanagan³

Abstract.—We used 20 0.25-ha fenced plots to experimentally study microhabitat use by 11 desert rodent species in southeastern Arizona. Removal of the largest granivore, *Dipodomys spectabilis*, produced the most pervasive shifts in the use of microhabitats while adding food or removing ants produced few responses. These results support the idea that this community is organized around competitive interactions involving aggression, preemption, and relegation.

It is generally believed that species have different fitnesses in different habitats, that most communities are comprised of sufficient habitat variation over which fitness differentials can be expressed, and that species select habitats that maximize their fitness (e.g., Levins 1962, Schoener 1971). The manner and degree to which species respond to the habitat template involves elements of selection in its purest form (i.e., choice), relegation, and correlation.

At the community level rarely do species occupy habitats in an ideal or cost-free fashion. By occupying space or using resources in a habitat specific manner organisms alter habitat suitability and thereby change the basis over which habitats are selected (Fretwell and Lucas 1970). Species that use limited resources in an efficient manner or are behaviorally dominant can monopolize the choicest habitats and relegate, directly or indirectly, subordinate or competitively inferior species to secondary

habitats (Colwell and Fuentes 1973, Bowers et al. 1987). If the capture success rates of predatory species varies among habitats this can also affect the absolute and relative fitness of prey species and their distribution among habitats (Kotler 1984, Bowers 1988).

Marked patterns of habitat occupancy and segregation are often cited as evidence that ecological communities are structured. The general pattern is that some (if not most) species in a community utilize habitats differently from random and differently than if each species occurred by itself. Observational and manipulative experiments have shown that dynamical properties of populations (including patterns of growth, demographics, and interaction) often become expressed as spatial phenomena, thereby establishing a connection between habitat occupancy and population dynamics (see Connor and Bowers 1987).

Many communities are comprised of an array of microhabitats which represent discrete, exploitable resources which occur with sufficient variability so as to be partitionable among species. The availability and distribution of microhabitats have been shown to limit the growth and density of many populations and, thereby provide an ecologically relevant and readily identifiable context over which species interactions and population growth can be studied (Price 1978, Rosenzweig 1981).

Desert rodents have long provided ecologists with a model system for examining the role of microhabitat in structuring communities. The basic pattern throughout the major North American deserts is that locally co-occurring species characteristically forage in microhabitats that are structurally distinctive with respect to perennial vegetation and soil type (Rosenzweig and Winakur 1969, Price 1978; for reviews see Brown et al. 1979, Munger et al. 1983, Price and Brown 1983).

Three mechanisms, alone or in combination, apparently account for the general pattern. First, because of differences in body size, mode of locomotion and behavior, rodents differ in their abilities to exploit particular distributions of food (i.e., seed) resources that are created by structural features of the microhabitat (Bowers 1982, Harris 1984, Price 1983, Reichman 1981). Second, rodents may differ in their ability to escape visually oriented predators so that the most susceptible rodents are limited to the safest microhabitats (i.e., under vegetative cover) while more vagile rodents show more unrestricted use of alternate microsites (Kotler 1984). Third, the ability of some species to aggressively defend areas from other rodents may be high in some habitats and low in others resulting in habitat dependent segregation involving domination/relegation (Hutto 1978, Frye 1983, Bowers et al. 1987).

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Desert rodent populations are remarkable in their ability to respond to short-term changes in the abundance and distribution of food resources; primarily seeds. Some of the more marked responses involve changes in use of microhabitats. For example, enriching microhabitats with supplemental seeds increases the use of these by desert rodents (Harris 1984, Kotler 1984, Price and Waser 1985). Such shifts are particularly noteworthy for microhabitats where the risk of being preyed upon is high, and suggests that both energetic profits and predatory risk play a role in determining which microsites are used (Hay and Fuller 1981, Price and Waser 1985, Bowers 1988). Food availability also can change the manner in which some rodent species interact: from competitive exploitative interactions under low levels of food to aggressive interference interactions under high levels of food (e.g., Congdon 1974).

In complex communities microhabitat use originates with preferences of individual species for certain microhabitats, but these basic responses may become altered, directly or indirectly, by interactions with other species. Moreover, at the community level it is not clear how changes in the resource base are manifest in patterns of spatial usage. Some important questions are: Does interspecific competition become more or less important with increasing food availability? Does the mode of competition change? How does food availability change the relative roles of preference and relegation in determining habitat occupancy? Thus, detailing the interplay between population and community-level responses to changes in resource availability should reveal much about the processes influencing microhabitat use and, thereby, the factors responsible for the organization of these communities.

In this paper we describe patterns of microhabitat use of 11 Chihuahuan Desert rodents over a span of

more than eight years. We experimentally manipulated both species composition and food supply and measured resulting shifts in microhabitat use. By detailing shifts in microhabitat use in response to our manipulations we were able to identify the most important interactions among species, estimate their relative strengths, and say something about the mode of interaction promoting the shifts.

Our results suggest that the organization of this community revolves more around differences in the ability of species to occupy and defend certain key microhabitats than changes in food availability.

Study Site and Methods

The present paper details changes in microhabitat use in response to long-term experimental manipulation of rodent composition and food supply. Our study site was located at an elevation of 1330 m in a relatively homogeneous desert shrub habitat on the Cave Creek Bajada 6.5 km east and 2 km north of Portal, in Arizona, USA. Manipulations were performed in twenty 0.25-ha plots. Each plot was fenced with 0.64-cm mesh hardware cloth, extending 0.7-m above and buried 0.2-m below ground. In addition to an unmanipulated fenced control (see below), the remaining treatments consisted of two general classes: treatments where one or more rodent species were removed, potentially changing both food availability and the potential for direct behavioral interactions; and food alteration treatments where supplemental millet seeds were added at a rate of 96 kg per year or seed-eating ants were removed. Experimental treatments were assigned to plots at random.

Fourteen rodent species of which 11 were commonly captured, inhabited the study site, all except those mentioned above had equal access to all plots (fig. 1). Because of problems

in consistently identifying the two *Onychomys* species (as either *O. torridus* or *O. leucogaster*) we group these together under the designation, *Onychomys* spp.

Sixteen equally-spaced gates in each plot allowed the selective exclusion of rodent species above a threshold body size while allowing all other species access. Access gates varied in size among the treatments. Large gates (3.7 x 5.7-cm) allowed all rodent species free access to control (2 plots), ant removal (4 plots), and the seed addition plots (8 plots; see below); medium-sized gates (2.6 x 3.0-cm) were used to exclude only the largest granivore, *Dipodomys spectabilis* (2 plots); and small gates (1.9 x 1.9-cm) were used to exclude all *Dipodomys* species (4 plots). The seed addition treatments included six plots where supplemental seeds were applied in 12 monthly applications (hereafter referred to as "constant seed additions"); two plots received the total allotment of seeds in three applications during the fall (September-November; referred to as "pulsed seed additions"). Seeds were uniformly scattered by hand over each plot.

It was estimated from productivity measurements at the site that the addition of 96 kg of seeds per year should have approximately doubled the total biomass of seeds produced annually (our estimate of seed production was ca. 400 kg/ha/yr). The constant seed additions included two plots where whole millet (*Panicum miliaceum*) was added (mean seed mass = 6 mg); two plots where cracked millet was added (mean mass = 1 mg); and two plots where an equal mixture of whole and cracked millet was added. The pulsed seed treatment was designed to represent a doubling of the seed production of summer annual plants, a particularly important food source for the rodents in this community (Davidson et al. 1985). Brown and Munger (1985) found no differences in responses of rodents to addition of

seeds of different size, so the four constant seed addition treatments will be lumped together here (6 plots).

Rodents were censused monthly during the week of the new moon (moonlight has been shown to effect the microhabitats used by desert rodents; Bowers 1988) using live traps placed in each plot in 7 x 7 grids with 6.5-m between trap stations. Traps were baited with millet and opened for one night per month with plot gates closed so that only plot residents would be captured. For more details concerning the experimental design, see Bowers et al. 1987, Brown and Munger (1985), and Brown et al. (1986).

Following the lead of many previous studies on desert rodent communities we used the percent cover of perennial plants to characterize the microhabitat at each of the 980 trap stations. Percent cover within a 2-m

radius of each trap station was measured by ocular estimation using reference disks of known percent coverage. Cover was measured in 1978, 1981, and 1983. There was no significant changes in perennial cover over this five year period (Mann-Whitney U-test; $P > 0.05$), so we used data from 1983 to characterize microhabitats. Table 1 summarizes vegetation cover data over the entire study site.

Fence installation was completed in June, 1977; premanipulative trapping was conducted from July-September, 1977; and the manipulations were initiated in October, 1977. We restrict our analyses to include post-manipulation data compiled from October 1977 to December 1984 and to only those 20 plots to which rodents had access.

Analyses were designed to answer two questions: first, what are the patterns of species associations occurring at the community level; and sec-

ond, what role does microhabitat play in the distribution of individual species. In this study patterns of association (including the association of rodent species with each other and with structural microhabitats) are analyzed at the level of individual trap stations (980 total). Hence, we

Table 1.—Mean percent cover of the seven most common perennial plant species over the study site (standard deviations in parentheses).

Species	% cover
<i>Acacia constricta</i>	1.5 (4.4)
<i>Ephedra torreyana</i>	2.7 (3.6)
<i>Florensia cernva</i>	2.7 (4.7)
<i>Gutierrezia lucida</i>	3.3 (3.9)
<i>Lycium andersonii</i>	0.4 (2.2)
<i>Mimosa biuncifera</i>	0.2 (1.4)
<i>Prosopis juliflora</i>	0.6 (4.5)
Total cover (all species)	12.7 (8.7)

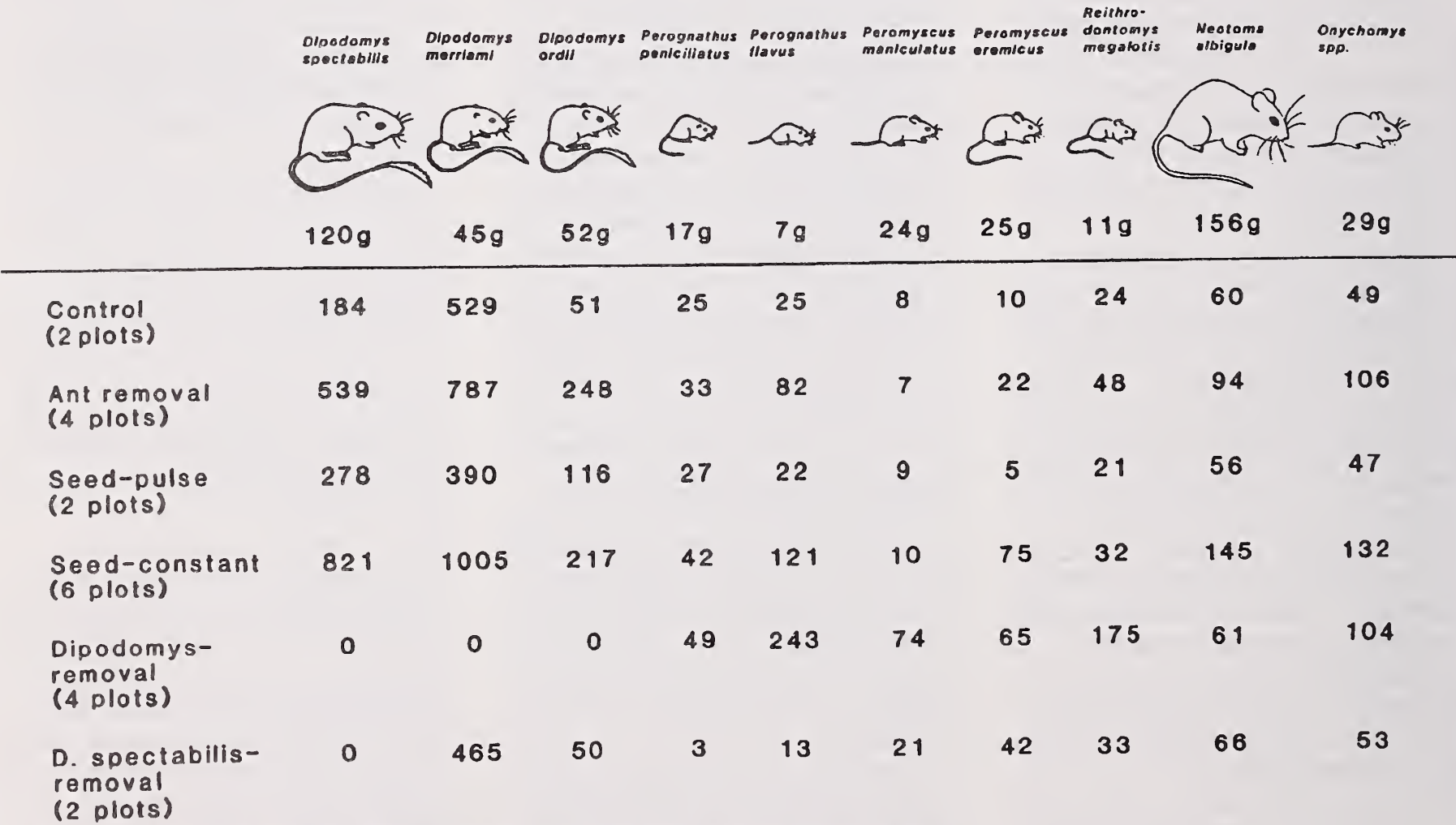


Figure 1.—Rodent species on study site (including their body sizes) along with their capture frequencies in each of the experimental treatments. Included are the number of plots in each treatment.

were interested in measuring responses of rodents to microhabitat variation occurring at a scale of a meter or two. However, we acknowledge that habitats may also be selected at larger spatial scales (Morris 1987). For example, rodents may also select areas on the basis of microhabitat composites (e.g., at the level of the home range) which might be best examined by considering structural microhabitats over trap station aggregates. However, there is reason to believe that even if selection does occur at these larger scales it is still oriented towards excluding or including certain key microhabitats. Hence, we were confident our analyses would detect patterns at both scales.

Indices of species association were calculated by using the frequency that species were captured at the same trap station using trap data for the eight year period. This involved several steps: (i) tabulating the proportion of trap stations where each species was captured over the eight year study; (ii) tallying the number of trap stations where each pair of species co-occurred; and (iii) comparing the observed frequency of co-captures to that expected if species captures were distributed independently and randomly among trap stations. The expected frequency of species co-capture was calculated by multiplying together the proportion of stations capturing species individually to generate a probability of joint occurrence. A modified chi-square statistic, including the sign of association, was then used as an index of association: i.e., a measure of the difference between the observed and expected values. The null hypothesis was that there would be an equal number of positive and negative associations with less than 5% of the association values being statistically significant at a $P = 0.05$.

The analysis described above can also be used to examine the association of all species in the community at individual trap stations. Specifi-

cally, instead of asking how frequently species pairs associate we can use the maximum likelihood estimation technique to estimate how many trap stations should have captured 0, 1, 2, . . . n species (where n is the number of species in the community) over the eight year period. As in the above analysis, this uses the proportion of stations capturing each species, multiplies these together in all possible combinations that might produce co-captures of from 0 to n species, and sums these probabilities for each number of possible co-captures to give an expected distribution over the population of trap stations. The null expectation here is that species captures are independently and randomly distributed among trap stations.

Analyses were also performed to examine the individualistic responses of species to variation in microhabitat and, particularly, how these change when manipulations are applied at the level of the entire community. We used percent cover by perennial plants at trap stations as a general descriptor of microhabitat type. Our goal was not to use a series of variables to explain the largest amount of variation in microhabitats where species were captured but rather we were interested in identifying a major resource axis over which both species distributions and community-level responses could be analyzed. Past work justified using cover as such a variable (Brown et al. 1979, Munger et al. 1983, Price and Brown 1983). Our scheme of categorizing microhabitats was simple: trap stations were grouped into those with greater-than-median and those with less-than-median cover. This was performed separately for stations in each of the six treatments. Hence, each microhabitat category was represented by an equal number of trap stations in each treatment type. The null hypothesis for analyzing the trap data was if rodents use microhabitats randomly, and without regard to vegetative cover, they should be

trapped in equal frequencies at stations in the two microhabitat categories. Avoidance or preference for microhabitats would be indicated by a disproportionate number of captures in one or the other category.

We were also interested in examining (1) the microhabitat affinities of species in the different treatments, and (2) shifts in types of microhabitats used by the same species over the different seasons of the year and over the six experimental treatments. In the first case we used the Fisher Exact Probability procedure in a two-tailed test of the null hypothesis that captures in the two microhabitats did not differ from a 1:1 ratio (Siegel 1956); in the second we subjected the proportion of species' captures in the two microhabitats to a 2-way ANOVA where season and treatment represented treatment factors.

Results

Results are based on 8,019 captures of the 11 most common rodent species. Figure 1 lists the frequency of capture for each species in the six treatments summed over the eight year study period.

Community-Wide Patterns of Microhabitat Use

What are the patterns of species association at the level of the entire community? In answering this we considered the frequency that species were captured at the same trap station. We performed two tests. We first calculated species associations for all possible pairings of the 11 species occurring in plots with intact rodent assemblages (i.e., those 14 plots with large gates) resulting in a total of 45 values of species association. Plotting all association values show that most species in this community are captured at the same station much less frequently than predicted by chance (fig. 2; the null hypothesis is that

there would be an equal number of positive and negative associations and that only 5% of these would be statistically significant at $P < 0.05$). The deviation from what is expected is particularly striking considering that 27 of the association values exceeded the cutoff value for significance (3.84 for $p < 0.05$ and d.f.=1) and all of these were in the direction of negative species associations; there was not a single significant positive association. This suggests a high level of organization revolves around the spatial segregation of species.

Among those factors that could be responsible for this marked segregation are unique habitat preferences of species. These could work alone or in conjunction with habitat segregation that is mediated through interactions with other rodent species. The design of our experiment allows a further examination of the role of species interactions in producing the pattern. Specifically, our experiment includes treatments with an intact rodent assemblage (14 plots; 686 stations) as well as treatments where either *D. spectabilis* (2 plots; 98 stations) or all *Dipodomys* (4 plots; 196 stations) were selectively removed and excluded. Because previous studies have shown *Dipodomys* (and especially *D. spectabilis*) to be behaviorally dominant over many of the species they co-occur with (Blaustein and Riser 1974, Frye 1983, Bowers et al. 1987) there is reason to think that by their removal the patterns of association of the remaining species may change. To evaluate this possibility we restricted the analyses to include just those eight non-*Dipodomys* species that occurred in all three treatments (number of pairwise association values for this group = 21). The degree to which these species were associated with each other at trap stations in each of the three treatments was calculated as before, and then compared across the three treatments (fig. 3). The results show that removing either all *Dipodomys* or just *D. spectabilis* significantly alters the

degree to which the remaining species are spatially segregated ($X^2 = 17.33$, $df = 2$; $P < 0.000$). While the trend is clearly towards more positive and fewer negative associations when competitors are removed, most of the species are still negatively associated with each other.

The previous analysis can be extended from the two-species case to one considering the association of all 11 species. Specifically, instead of asking how frequently species pairs associate we can use the maximum

likelihood estimation technique to estimate how many trap stations should have captured 0, 1, 2 . . . 11 species over the eight year period. Comparing the actual number of species captured per station with that expected (fig. 4) shows that the observed distribution is shifted to the left of that expected (significantly different at $P < 0.05$ using Kolmogorov-Smirnov one sample test), that there are significant differences in the mode of species co-captured per station (expected=4; observed=3), and

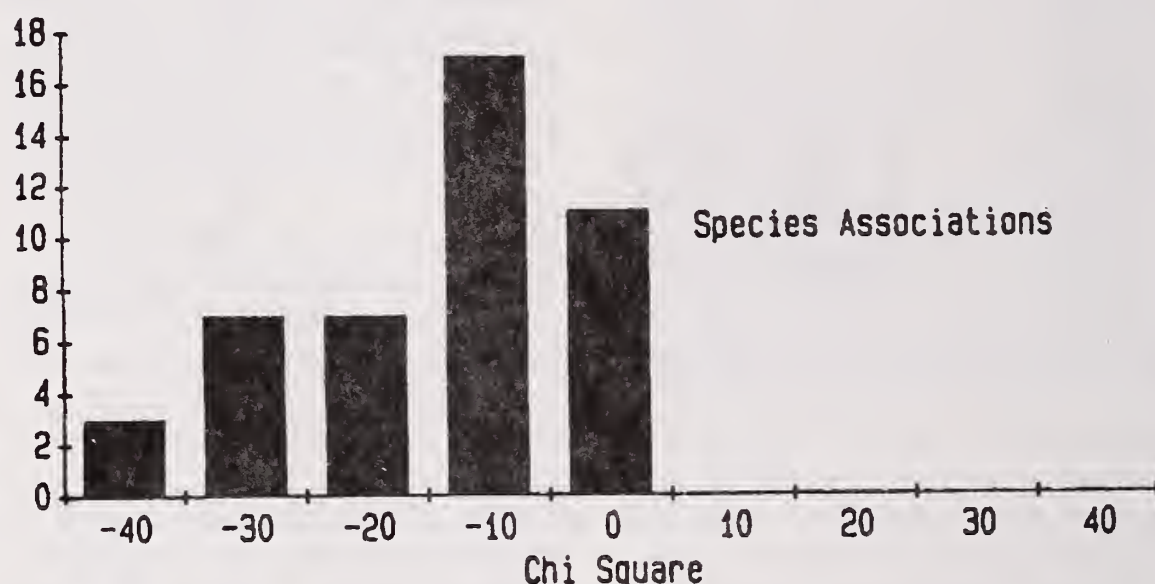


Figure 2.—Estimates of species associations for plots with intact rodent assemblages (i.e., those with large gates). Association values represent modified chi-squares (with the sign of association) and were calculated according to whether species were captured at the same trap station more or less frequently than expected by chance. See text for more detail.

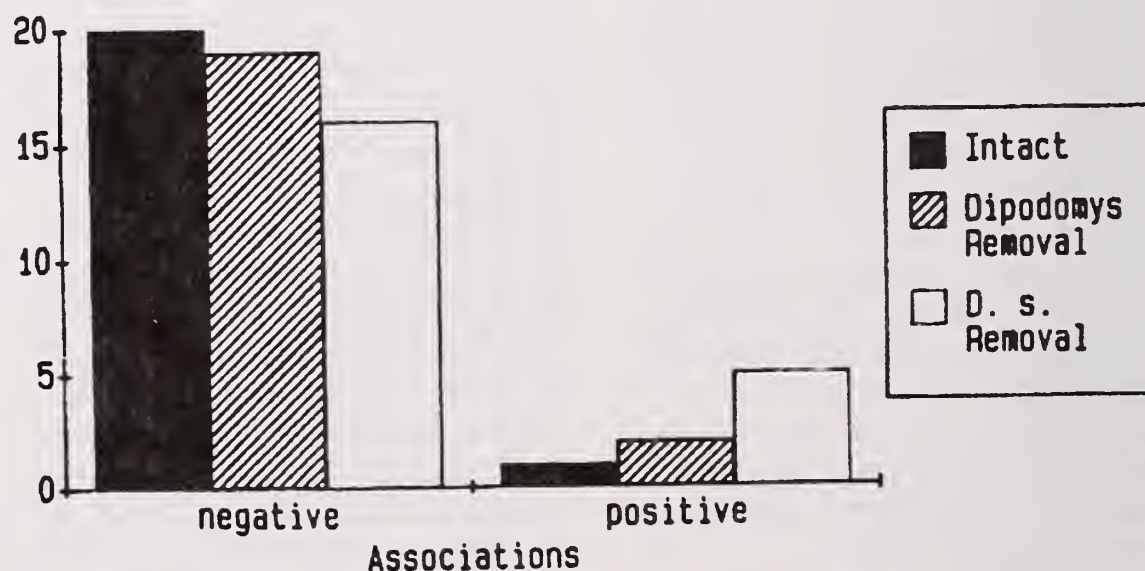


Figure 3.—Histogram of the number of positive and negative species associations for non-*Dipodomys* species broken into three treatment categories: (i) treatments with intact rodent assemblages; (ii) *D. spectabilis* removal plots; and (iii) *Dipodomys* removal plots.

that there are large differences in the proportion of stations capturing two species (ca. 5% for the expected compared to 23% for the observed). The main result is that trap stations captured fewer species than expected if species captures were random, which further evidence that species in this community are spatially segregated.

Use of Space by Individual Species: The Role of Cover

In this section we are interested in the individualistic responses of species to microhabitat variation and, particularly, how these change when manipulations are applied at the level of the entire community.

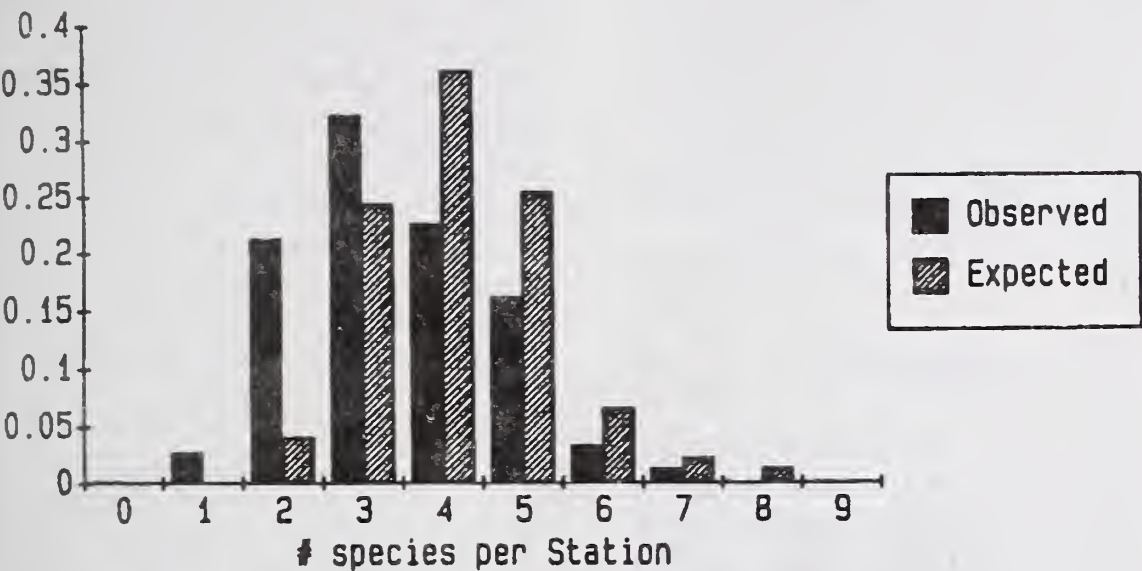


Figure 4.—Histogram of expected and observed number of species captured at individual trap stations.

There was marked variability both within and between species in the usage of microhabitats (table 2 and figs. 5 and 6). On control plots *Peromyscus eremicus*, *Neotoma albigula*, *Reithrodontomys megalotis*, and *Dipodomys merriami* (in all treatments but the *D. spectabilis* removals) all showed positive associations for trap stations with greater-than-median cover.

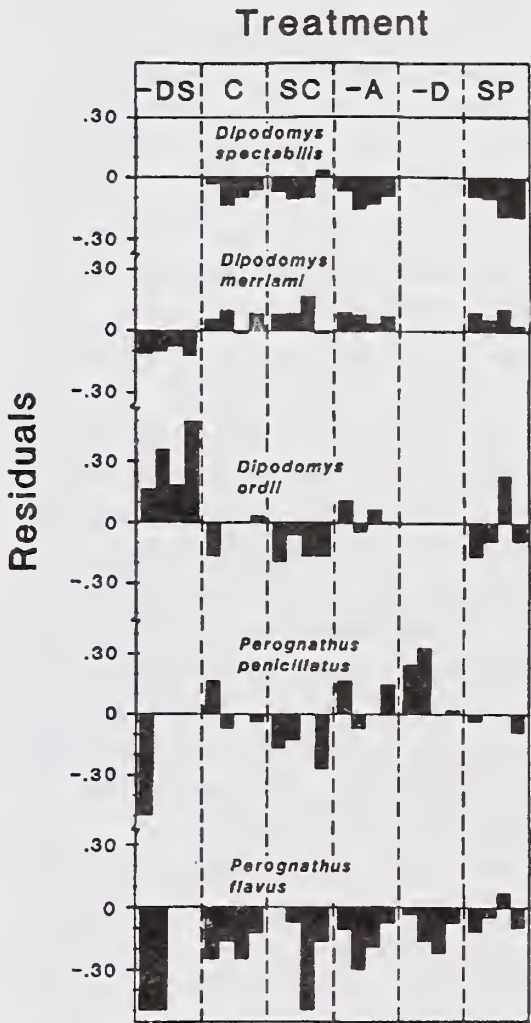


Figure 5.—Distribution of captures in greater-than and less-than median cover for the five heteromyid species listed according to treatment and season. Capture data is graphed relative to what the null hypothesis predicts (i.e., an equal number of captures in both microhabitat types; the zero line). Preference for higher-than-median sites is represented by positive values; less-than-median cover by negative values. Bars within treatment categories indicate season: from left to right Spring (March-May), Summer (June-August), Fall (September-November), Winter (December-February). Treatment designation is as follows: “-DS”, *Dipodomys spectabilis* removal; “C”, control; “SC”, constant seed addition; “-A”, ant removal; “-D”, *Dipodomys* removal; “SP”, pulsed seed additions.

Table 2.—Results of analyses testing for (i) microhabitat associations of species in control plots and (ii) for shifts in microhabitats between control and experimental plots. Microhabitat associations of species in the unmanipulated community are indicated under the “control” treatment: “c” if they were trapped significantly more often in greater-than-median cover; and “o” if more often in lesser-than-median cover. Significant shifts in microhabitat use relative to that on “controls” are indicated by a “+” if the shift was towards high cover and “-” if towards low cover (more open) sites. “R” is used to indicate which species were removed from treatments; “*” indicates the level of statistical significance (* for $P < 0.05$; ** for $P < 0.01$).

Species	Treatments					
	Control	Seed pulsed	Seed constant	Ant removal	D.s. removal	D. spp. removal
<i>D. spectabilis</i>	o				R	R
<i>D. merriami</i>	c				-**	R
<i>D. ordii</i>					+**	R
<i>P. penicillatus</i>			-*		-*	+
<i>P. flavus</i>	o				-*	
<i>R. megalotis</i>	c			+*	+*	
<i>P. maniculatus</i>			+*		+*	
<i>P. eremicus</i>	c				+*	
<i>N. albigula</i>	c				-**	
<i>O. spp.</i>						

Those species associated with more open microhabitats included the large kangaroo rat, *Dipodomys spectabilis*, and the smallest species, *Perognathus flavus*. The remaining species used the two microhabitats more indiscriminantly with the exception that *Peromyscus maniculatus* was captured more frequently in high-cover microsites in the *D. spectabilis* removal treatment.

Figures 5 and 6 and table 2 show our experiments were of the kind and were of sufficient intensity to promote community-wide changes in the use of microhabitats by all species; only the *Onychomys* showed significant seasonal shifts in microhabitat use (captured more frequently in higher-cover areas during the fall than in the other seasons). Using the control treatment as a reference point showed that the majority of species shifted their use of microhabitats on plots where *D. spectabilis* was experimentally removed. These shifts, involving eight of the nine species present, included an increase in the use of microsites with less-than-median cover by *D. merriami*, *P. pencillatus*, *P. flavus*, and *N. albigula*, and an increase in the use of high-cover sites by *P. maniculatus*, *P. eremicus*, *R. megalotis*, and *D. ordii*.

The remaining manipulations registered fewer and less dramatic shifts: i.e., increased use of open microhabitats by *P. pencillatus* and *P. maniculatus* on constant seed addition plots; and shifts towards higher-cover microsites by *R. megalotis* and *P. pencillatus* in ant removal and *Dipodomys* removal treatments, respectively.

The role of microhabitat in the organization of this community can be further evaluated by comparing the distribution of trap captures for all species with what is available at trap stations (fig. 7). The objective was to determine whether certain types of microhabitats are used by the rodent community more frequently than others. This analysis shows that the distribution of captures in control, *D.*

spectabilis removal, and *Dipodomys* removal plots all differ significantly from that expected if the use of microhabitats was random with respect to vegetative cover (Kolmogorov-Smirnov two sample test; $P < 0.05$). However, there are characteristic ways these differ from expected. On control plots there were fewer than expected rodent captures in traps having $< 5\%$ cover; on *D. spectabilis* removal plots there were a greater-than-expected number of captures for this same cover category; and on *Dipodomys* removal plots most rodents were captured at trap stations with $> 10\%$ cover.

Discussion

Our results identify species interactions as the principal factor producing structure in this community. It is significant that, by adding supplemental seeds or removing ants, we were able to change microhabitats used by only a few of the species but removing a large, potentially dominant competitor produced many shifts. This suggests that the primary mode of interaction, as it effects the patterns of microhabitat use in this community, involves the direct responses of rodent species to each other rather than interactions mediated through the exploitation of food resources, or the individualistic responses of rodents to particular microhabitat types.

The results point to the importance of one dominant species, *D. spectabilis*, whose presence in the community plays a disproportionate role in determining which microhabitats are utilized by the other species, and thus the organization of the community as a whole. Whenever it is present, regardless of how much food is available, it appears to relegate the majority of other rodent species to higher-than-median cover habitats, thereby reducing the density of potential competitors in the open habitats it prefers. A notable

exception is *Perognathus flavus* which was captured in open sites along with *D. spectabilis*. Because of its small size (ca. 7 g) and low population density, *P. flavus* may have only a negligible impact on the food resources that can be harvested by *D. spectabilis* and, therefore, may not compete directly with or be subjected to its aggressive behavior. The importance of such size-ratio thresholds in allowing species to coexist has been discussed (Bowers and Brown 1982). Defending open areas from other rodents may be a mechanism by which *D. spectabilis* is able to preempt food resources for its exclusive use. Supporting evidence for this comes from other research at our study site where it was found that

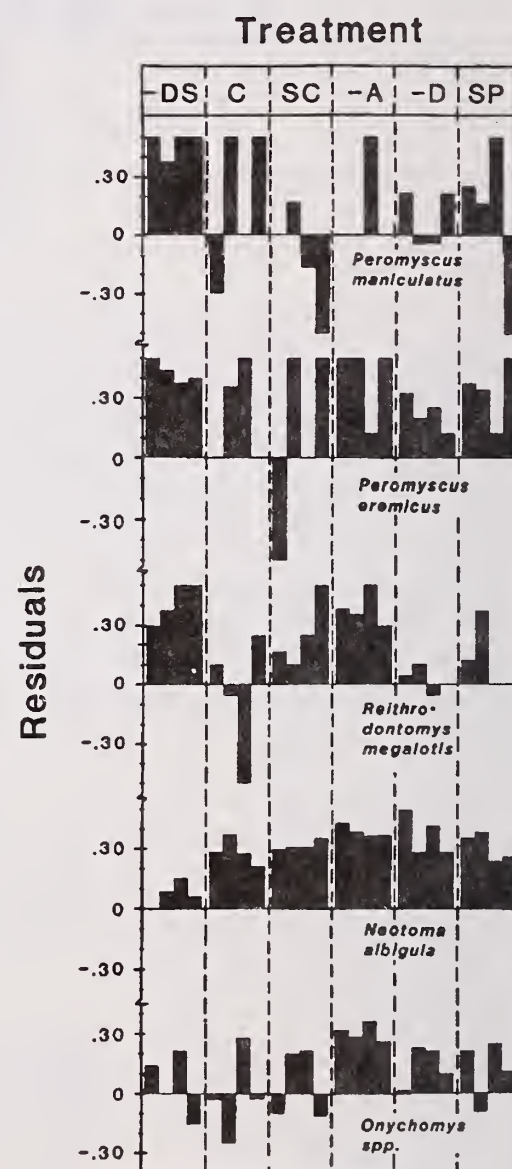


Figure 6.—Distribution of captures in the two microhabitat categories for the six Criceid rodents listed by treatment and season. See legend to figure 5 for more details.

experimental seeds placed in open microhabitats remained largely unharvested when *D. spectabilis* was present but quickly disappeared in plots where it was removed (see Bowers et al. 1987).

Our results also infer something about the mechanism by which *D.*

spectabilis affects the use of space by other rodent species in the community. Competition can be mediated through two processes: (i) exploitative interactions where species interact through a shared resource base; or (ii) contest interactions involving aggressive dominance and relegation

to suboptimal areas and resources. For exploitation alone to account for the patterns of microhabitat use, *D. spectabilis*, through its foraging, would have to significantly alter the distribution of food (seed) resources among the microhabitats in ways that are ecologically significant for the other species. This is unlikely for several reasons. First, many of the seeds utilized by the smaller species appear to be too small to be economically harvestable by *D. spectabilis* (see Bowers et al. 1987). Second, many of the species showing significant microhabitat shifts were non-granivores (i.e., *Neotoma*), and hence, should be relatively insensitive to changes in the resource base attributable to the foraging of *D. spectabilis*. Third, adding seeds should have made food more available to all species and reduced the degree to which *D. spectabilis* was able to alter the distribution of food resources, so that shifts by the other species would have been expected in response to this treatment. Moreover, significant changes in the distribution of food resources were more likely to have been caused by *D. merriami* that occurs at higher densities than *D. spectabilis*. Our results show that adding supplemental seeds or removing *D. merriami* produced fewer shifts than removing just *D. spectabilis*.

As an alternative to exploitation, competitors of large body size may directly restrict the foraging activities of smaller species through interference. Under an interference mode of competition adding seeds may not alter the intensity or outcome of the interaction. Because most significant shifts in microhabitat use occurred in the *D. spectabilis* removal treatment—coupled with the fact that adding seeds had little effect on the patterns of microhabitat—leads us to the conclusion that aggressive interference by *D. spectabilis* is the mechanism most consistent with our results.

Our study also indicates that the majority of shifts in microhabitat use originate with the *D. spectabilis*-*D.*

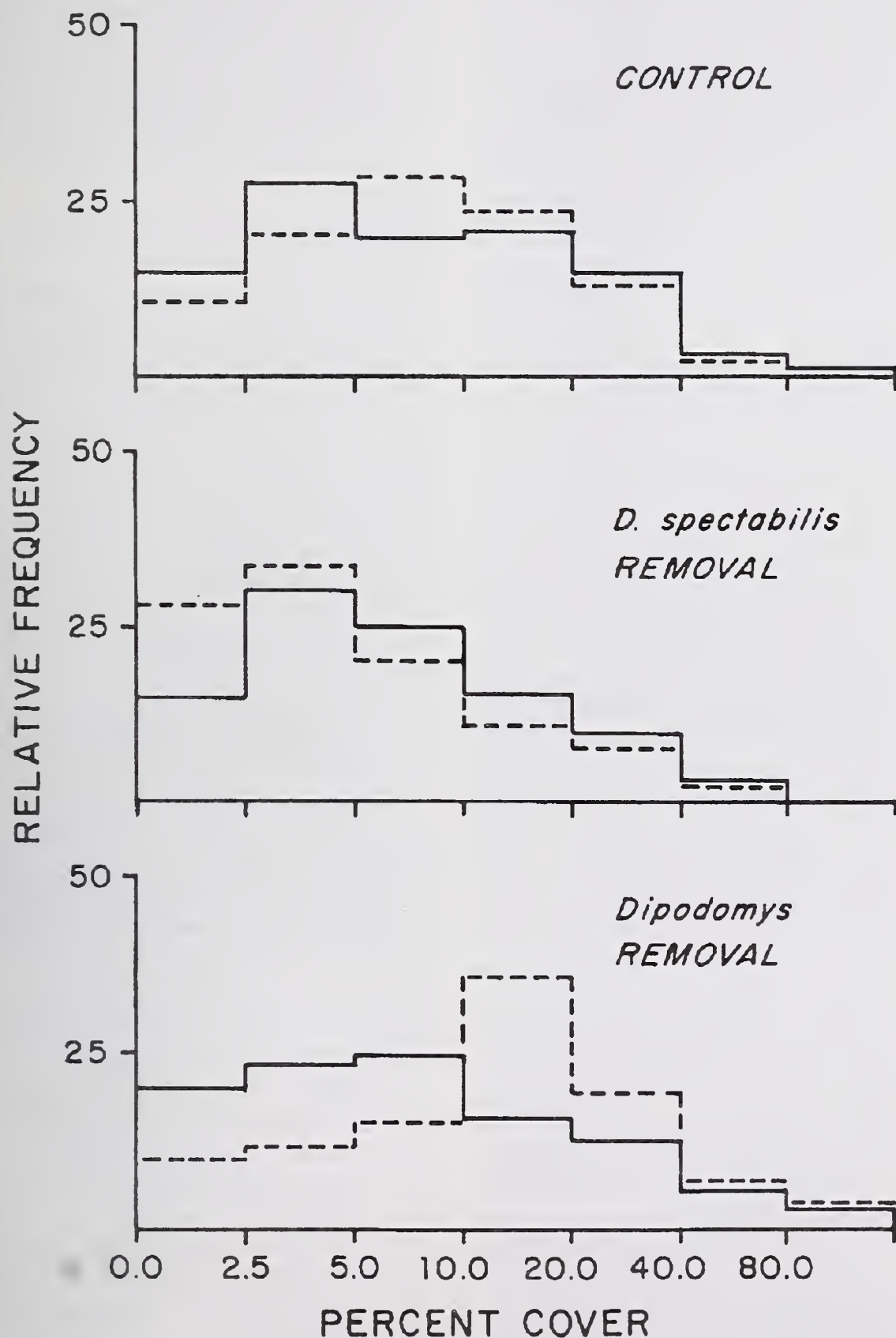


Figure 7.—Distribution of trap captures (broken line; all species combined) and available trap sites (solid line) relative to vegetative cover on (i) control; (ii) *D. spectabilis* removal; and (iii) *Dipodomys* removal plots.

merriami interaction and, at the community level, this one interaction affects the microhabitat utilization of the majority of rodent species through a complex network of direct and indirect interactions. Perhaps the most striking shift (not in the magnitude of response but in the number of individuals involved) was the increased use of open areas by the numerically dominant *D. merriami* when *D. spectabilis*, which had formally used these sites was removed. Most other shifts by the smaller rodents, including the increased use of open microhabitats by *Perognathus flavus*, *Peromyscus maniculatus* and *Reithrodontomys megalotis* when all *Dipodomys* were removed, suggest that these species responded directly to *D. merriami* and only indirectly to *D. spectabilis*. Hence, there appears to be a hierarchy of interactions. The primary one is between the behavioral (*D. spectabilis*) and numerical (*D. merriami*) dominants and it is this interaction around which the community is organized. Other studies have noted the potential for interference between desert rodents (Blaustein and Riser 1974, Hutto 1978, Rebar and Conley 1983), especially between *D. spectabilis* and *D. merriami* (Frye 1983), and our study shows how this one interaction can resound throughout the community to affect many other species.

A primary motivation for our study—and most studies focusing on the role of habitat—is that microhabitats represent a limited and exploitable resource and the manner in which they are used directly impinges on population growth and density. Many of the experimentally induced microhabitat shifts we have reported were accompanied by changes in local species density (Brown and Munger 1985, Brown et al. 1986) that support the contention that *D. spectabilis* controls the dynamics of this community through a combination of direct and indirect effects. For example, increasing food levels by adding seeds resulted in an in-

crease of *D. spectabilis* and a decrease in *D. merriami* densities. Removal of *D. spectabilis* resulted in positive density compensation of *D. merriami* but no changes in densities of the smaller seed-eaters; removal of all *Dipodomys*, however, resulted in large density increases in several of the smaller rodents. Taken together, the microhabitat and density responses to our manipulations indicate that interference competition for certain foraging sites not only determines the spatial organization of this community but that it is directly involved in the regulation of rodent densities.

There are several aspects that warrant further comment. First, our results show that when *D. spectabilis* is present open sites are underutilized by the community as a whole; when *D. spectabilis* is removed the remaining *Dipodomys* shift to use these open sites; but when all *Dipodomys* are removed the remaining species are unable to fully utilize the vacated microhabitats (fig. 7). Hence, there appears to be a limit to how far the community can compensate for the absence of certain species. Among the possible explanations for this might be that assemblages of desert rodents have been associating together for a sufficient time to have lost the flexibility to respond to situations where one or more of the species are absent (Schroder and Rosenzweig 1975). Another is that quadrupedal species may have a limited ability to avoid predators in open microhabitats and this limits the degree to which they can compensate when the bipeds are removed. In either case the relaxation of one factor (in this case the removal of dominant competitors) appears to be accompanied by the increased importance of others.

Second, the effects of interference competition by *D. spectabilis* appear to be effective in excluding interspecifics primarily in open areas although this dominant does occur in greater-than-median cover habitats. It may be that aggression is of lim-

ited value in bushy microsites where subdominant species may readily find refugia. As a result, *D. spectabilis* may be involved in two kinds of interactions with each of its competitors; exploitatively for seeds in bushy sites and through interference in open microhabitats. As a result, the highly asymmetrical interactions between the dominant/subordinates in open sites may become more nearly symmetrical in bushy sites where premiums are on foraging efficiency.

Third, the existence of strong, aggressive interactions among species increases the potential for indirect and high-order interactions that involve species that overlap very little in resource utilization. For example, the large herbivore, *Neotoma albigula* was as likely to shift its microhabitat use as the granivorous species. However, it is interesting to note that although the non-granivores shifted microhabitat use when granivorous species were removed, significant density changes were limited to just other granivores (Brown and Munger 1985). Hence, while interference may play a role in determining use of microhabitats by rodents in several foraging guilds, its effects appear to be most significant for ecologically similar species.

The goal of experimental programs is to hold most variables constant while manipulating others, and then to measure for shifts in response variables. In this paper we have used patterns of microhabitat use in control plots as a reference point for interpreting our experimental results. The assumption in doing this is that the degree to which the community responds to a particular manipulation provides an estimate of its importance in producing the basic pattern. In our particular case we wanted to know how the baseline patterns of microhabitat use (i.e., those in control plots) change when supplemental food is added or species are removed. While some of our patterns are easy to interpret, others are very complex and appear to in-

volve a hierarchy of responses that operate over different scales in time and space. The existence of such a dynamic and diverse set of responses shows the limitations of most two-species models of interspecific interactions upon which past theories of community organization have largely been based; they also call into question the value of studies seeking to understand the mechanistic processes that determine community composition through comparative, nonexperimental methods.

Implications for Management

While the spatial association of small mammals with particular microhabitats has been rigorously and repeatedly documented, and the patterns suggest almost a universal role of microhabitat in "structuring" small mammal communities, the processes responsible for producing these associations are poorly understood (Price and Brown 1983, Bowers 1986). To successfully manage/manipulate such communities there is a clear need to better understand the processes that determine which microhabitats are used and which are not. Towards this end we identify two particularly relevant areas for our discussion: (1) the scales in time and space over which microhabitat use occurs; and (2) the roles of correlation, and selection/relegation in the occupancy of microhabitats.

Vagile organisms, e.g. small mammals, can potentially respond to features of the habitat at several different scales. At the macro-end of the habitat spectrum animals choose areas in which to establish home ranges. Microhabitat selection, in contrast, usually involves the use/disuse of small areas within the home range. There are also temporal differences in schedules of usage: macrohabitat selection occurs over a much longer timescale (weeks-months) while microhabitat use occurs more immediately (seconds-

minutes). While it was assumed for years that macrohabitat selection occurred through the selection of composite microhabitats, recent work on small mammals suggests that the two may be largely separate (Morris 1987).

Most factors that are demonstrably important to the structure of small mammal communities, i.e., primary productivity, plant species and foliage height diversity, vegetation cover, substrate type, competitor diversity and abundance, and predatory pressure, vary more between macrohabitats than among microhabitats within particular locales. For example, primary productivity and plant cover are determined by plant species composition and general conditions for growth that vary over large environmental gradients at the macrohabitat scale. These large scale gradients influence patterns of microhabitat use by determining which rodent species are present, their densities, the distribution and abundance of food resources, and the types of microhabitats that are available for selection. As a consequence, the composition, densities and demographical behavior of small mammal populations and communities may more closely reflect habitat variability at the macro—rather than the micro—scale. On the other hand, microhabitat usage is a phenomena involving choices of individuals. Microhabitats that, by definition, vary over scales smaller than individual home ranges, have significance for the survivorship or reproduction of foraging individuals, but may have little relevance when integrated over the population as a whole.

Most experimental studies examining the role of microhabitat in structuring small mammal communities tend to confound micro- and macrohabitat effects. Typically, manipulations (e.g., food addition, species removal, tailoring of vegetation) are applied at the level of the macrohabitat with microhabitat usage by individuals measured as a response

variable. The research reported here suffers from such a confounding. Other field experiments that examine the allocation of foraging time among patches restrict manipulations to the level of microhabitats (Kotler 1984, Price and Waser 1985), and are not confused by responses of entire populations. Clearly, the time has come to utilize the information we now have to design comprehensive studies that distinguish between micro- and macrohabitat selection: i.e., studies that manipulate certain microhabitats on a scale over which populations might respond.

Correctly gauging the scale over which species respond to the environmental mosaic is critical to the successful management of that species. Programs aimed at managing species by manipulating microhabitats may or may not be successful depending on the scale at which the manipulation is applied. If the goal is to manage populations then macrohabitat may be the correct context for the program. This is not to suggest that microhabitat is an inappropriate context for management programs. What it does suggest is that management oriented programs should be directed towards populations rather than the behavior of individuals. In many cases this may involve changing the focus from the micro to macro level.

Our second point for discussion involves habitat correlation versus selection/relegation. Habitat usage is determined by the habitats available, the tolerances/preferences of organisms for these habitats, and the among-habitat variability in fitness. Clearly, there must be some variability in the structure of the habitat in order for selection to occur. Habitats that are relatively homogeneous at the smaller scales may not exhibit habitat associations even by highly selective species. Conversely, showing that a habitat has a significant degree of microhabitat variability does not imply that organisms have the ability or inclination to respond

to that variability. In order to apply the patterns of microhabitat use from one site to predict what is occurring at another requires an understanding of the biological factors underlying microhabitat use. Achieving this has proved difficult because of several problems. First, it is clear from a growing body of experimental work (including the present study) that habitat association does not necessarily imply habitat selection. Because microhabitats are rarely discrete, usually grade from one type to another, and involve a suite of factors that either characterize or are correlated with specific microhabitats, it is rare that habitat occupancy can be tied to a single factor. As a result it is difficult to conclude that an animal is selecting a habitat per se, some feature of that habitat, or some factor that is only correlated with that microhabitat. As a complicating factor habitat selection probably reflects integrated responses of organisms to maximize fitness relative to several largely independent processes. For example, animals might select microhabitats so as to minimize predatory risk, or food encounter rates, or to jointly maximize food intake while minimizing predatory risk (Bowers 1987).

Second, the present results and those of others (Price 1978, M'Closkey 1978, Wondolleck 1978, Bowers et al. 1987) show that microhabitat provides a template over which species interactions and competitive hierarchies become expressed. The pattern is one of selection/relegation—the competitive dominant selecting its preferred microhabitat and through exploitative or interference competition relegating other species to less preferred sites. The more ecologically similar two species—and hence, the greater the intensity of competition between them—the greater the potential role of interspecific competition in determining microhabitat usage.

Competitive interactions represent dynamical processes impinging on

microhabitat association and usage. Seasonal or year-to-year fluxes in resource availability or changes in the distribution of resources among microhabitats can alter the economical basis underlying competitive interactions, and thereby promote shifts in microhabitat usage. For example, Congdon (1974) found during periods of low resource availability that the large *D. deserti* and the smaller, *D. merriami*, coexisted in the same microhabitats but that the former became aggressive and excluded the latter from these sites when food levels increased. Similarly, Frye (1983) found that *D. spectabilis* excluded *D. merriami* from areas around its burrows just in the fall when seeds from summer annuals were abundant.

Competitively based selection/relegation has the effect of increasing usage of secondary habitats while decreasing usage of the most preferred ones. The result is that competition promotes the segregation of species among microhabitats and the degree to which the community is spatially organized. Thus it is no accident that the most striking patterns of microhabitat use and segregation are in communities that are highly competitive (Connor and Bowers 1987). As the present study has demonstrated even one strong interaction involving just two species (in this case the behavioral and numerical dominants) can affect microhabitat usage by all species in the community through direct and indirect pathways of interaction.

Care must be taken when examining the spatial organization of communities where competition might be occurring. Efforts to understand microhabitat utilization through reconstitution studies that measure individual species preferences for microhabitats, then combines these in a general model of microhabitat association, will miss higher-order competitive effects that may be the main determinants of microhabitat use. Further, since competition can be indeterminate, work over complex

pathways, and operate over widely varying scales in time and space it is doubtful that any one model can be used to predict microhabitat use over all communities. As a first step towards using microhabitat utilization as a tool for management programs we need to know which communities are interactive (i.e., structured around selection/relegation schemes), which are non-interactive, and something about ecological attributes of each. It may be that in some communities microhabitat is the correct context for management programs while in other communities the focus should be on species interactions. Species removal experiments such as the one described here provide a straightforward test of these models.

What we are suggesting here is that microhabitat use be viewed as a manifestation of process and that these processes provide the basis for management. We feel that the most important question is not which habitats are being used by a particular species but why it is using that microhabitat and not others. Recent work has shown that the pathways by which species interact at the level of ecological communities can be very complex and that similar patterns of microhabitat usage need not share a common sequence of causation (see papers in Diamond and Case 1986).

Without knowing something about which processes are locally important it is risky to extrapolate findings from one site in managing another. For example, Bowers (1986) found in rarefaction studies of the same three species rodent community that microhabitat use at one site was affected by interspecific competition but not at two others. Such results underscore the fact that microhabitat use involves multidimensional responses of organisms to their environment. Understanding the basics of such relationships should be the goal of community ecologists and managers alike.

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Response of Small Mammal Communities to Silvicultural Treatments in Eastern Hardwood Forests of West Virginia and Massachusetts¹

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Small mammals (i.e. New World mice, voles and jumping mice [*Crice-tidae* and *Zapodidae*], shrews [*Soricidae*], and squirrels [*Sciuridae*]) are an important component of north-eastern forest ecosystems. Their positions in the food web are broad, functioning as foragers on plant and faunal biomass and as prey to numerous predators. Small mammals play an important role in forest dynamics by dispersing seeds and mycorrhizal fungal spores and by enhancing organic matter decomposition and mineral cycling (Spurr and Barnes 1980).

Relatively little is known of the response of small mammals, by species and as a community, to silvicultural treatments of northeastern hardwood forests. Several studies have shown that the response varies by species but that the small mammal community is generally resilient to forest harvesting (Healy and Brooks 1988, Kirkland 1977, Lovejoy 1975, Clough 1987, Monthey and Soutiere 1985). These studies report the predominant effect of silvicultural treatments on small mammal habitat is the enhancement of the

ground cover and lesser woody vegetation. Stenotopic species sensitive to understory plant cover and its influence on microclimate seem to be encouraged, at least temporarily, by most forest harvesting, while eurytopic species seem unaffected.

The study began in West Virginia (WV), where one field season was completed, and was continued in Massachusetts (MA). Our objective was to investigate the response of the small mammal community, as characterized by live-trapping statistics, to standard eastern hardwood silvicultural treatment (Marquis et al. 1975, Hibbs and Bentley 1983). In WV, we studied the effects of even-aged regeneration clearcutting and subsequent succession on small mammal trapping data. In MA, the silvicultural treatment was intermediate thinnings, with a second interactive treatment of differential white-tailed deer density.

STUDY AREAS

The WV study sites were on the Cheat Ranger District, Monongahela National Forest. Three randomly located stands in each of four stand-age classes were studied to evaluate the small mammal community over a silvicultural rotation for even-aged management of a northern hardwood forest. The four age classes were seedling (8-9 years), sapling (12-14 years), sawtimber (61-76

Abstract.—We studied small mammal communities and associated habitats in West Virginia and Massachusetts hardwood forests with different silvicultural treatments. In Massachusetts, white-tailed deer (*Odocoileus virginianus*) density was a second interactive treatment. Total capture rates were relatively stable across all treatment classes. Small mammal community composition and individual species capture rates varied according to treatment. White-tailed deer density had a greater effect on the small mammal community than did silvicultural practices.

years), and mature (>100 years). The 12 stands averaged 19.4 ha and ranged in area from 6.1 to 38.8 ha. The study area is described in Healy and Brooks (1988).

The MA study sites were on the Quabbin Reservation in Franklin county. This watershed is managed by Boston's Metropolitan District Commission for water production. Four randomly selected stands in each of four treatment classes were studied to evaluate the interactive effects of intermediate thinning and white-tailed deer density on a southern New England oak forest's flora and fauna. The treatments were combinations of thinned vs. unthinned and low (6-8/mi²) vs. high (34-59/mi²) deer density. The 16 stands averaged 19.1 ha and ranged in area from 4.9 to 57.5 ha. The MA study site is described in Healy et al. (1987).

METHODS

Small Mammals

Small mammals were live-trapped at 10 systematically located stations along a transect in each of the 28 stands. Transects were located along the long axis of each stand. Trap stations were no less than 80 m apart in any stand. At each station three Sherman-type box traps (7.6 X 7.6 X 30.5 cm) were baited with a mixture of peanut butter, rolled oats, and bacon fat and set within 1 m of each station.

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Traps were set for three successive nights, left closed for one (WV) or four (MA) nights, and then set for three additional successive nights. Sprung traps were noted and their numbers subtracted from the total number of trap nights per station (18) to calculate the number of effective trap nights. Each forest stand was trapped once per year. Mammals were trapped from mid-September to early October 1981 in WV. Mammals were trapped during June and July of 1985-87 in MA. Captured mammals were marked for individual identification and released.

Vegetation

Vegetation sampling techniques varied between states. Vegetation plots were systematically located along the same transects as were the small mammal trapping stations. In WV, trees (≥ 2.5 cm) were sampled using point-centered-quarter method (Cottam and Curtis 1956), while in MA, trees were sampled using fixed-radius plots. Herbaceous and woody-stemmed understory, including trees ≤ 2.5 cm, were sampled in WV using the line intercept method (Eberhardt 1978) and in MA, these flora were sampled using fixed-radius plots. Tree and understory sampling occurred at the same locations along

the transects. These data were used to estimate tree density, dominance, and average diameter and understory cover by major plant life form (i.e. forb, fern, graminoid, and woody-stem species).

Analysis

Small mammal trapping results and vegetation samples were summarized by treatment class and forest stand. Treatment effects on small mammal capture rates, standardized as captures per 100 trap nights (TN), were analyzed by one-way (WV) or two-way (MA) analysis of variance in a balanced, nested design with stand sum-of-squares the error term for treatment effect. Treatment effects on species composition of small mammal capture rates were analyzed using multivariate analysis of variance. Testing of treatment effects was done using the SPSS MANOVA procedure (Hull and Nie 1981).

RESULTS

Vegetation Structure

West Virginia

Tree density declined and both basal area and average tree diameter in-

creased as the forest stands matured from an even-aged regeneration harvest (table 1).

The understory changed more in life form composition than in total cover. Forb cover increased in percentage of cover with stand-age as did ferns while shrub cover declined (table 1). All forest stands supported a luxuriant understory regardless of age.

Massachusetts

Tree density and basal area decreased with thinning while average tree diameter changed little (table 1). The effect of deer density is understandable if one considers the low deer-unthinned treatment to be a "control" condition.

From this perspective, high deer-density stands had lower tree density and basal area, and a larger average diameter because of poor regeneration resulting from browse damage (table 1).

Forb cover declined with higher deer densities, while graminoid cover increased (table 1). Shrub and fern cover responded irregularly to the treatments except for a dramatic increase in fern cover in high deer-thinned stands, an effect reported elsewhere (Marquis 1987).

Table 1.—Average structural characteristics of sampled forest stands by state and treatment class.

Characteristic	West Virginia				Massachusetts			
	Seedling	Sapling	Sawtimber	Mature	Low Deer		High Deer	
					Unthinned	Thinned	Unthinned	Thinned
Tree stems ≥ 2.5 cm								
Stems/ha	1970	2482	969	772	1334	876	974	645
Basal area (m ² /ha)	5.3	12.3	41.7	35.9	24.5	15.7	22.8	15.7
Average diameter (cm)	5.2	6.8	17.9	17.6	12.2	10.7	13.5	13.5
Percent understory cover								
Forb species	17	18	18	36	18	16	7	14
Fern species	5	11	21	14	15	13	12	32
Graminoids	2	2	<1	<1	1	2	5	17
Shrubs and trees < 2.5 cm	32	17	9	9	15	31	26	26

Small Mammals

West Virginia

In the one trapping season, 662 individuals of 15 species were captured. Total capture rate averaged 33.2 individuals/100 TN. Average total capture rate declined with stand-age, from 42.4 individuals/100 TN in seedling stands to 27.4/100 TN in sawtimber stands, and then increased to 31.0/100 TN in mature stands (table 2). The effect of stand-

age class on total capture rate was not statistically significant ($F = 3.16$, $P = 0.086$, d.f. = 3,8).

Six species were captured in all four forest age classes, eight additional species were captured in three or fewer treatment classes (table 2). Species richness was greatest in the sawtimber stands, intermediate in the younger stands, and least in the mature stands.

The southern red-backed vole (see table 2 for small mammal scientific nomenclature) was the most com-

mon species, averaging 12.7 individuals/100 TN. Capture rate for this species declined with stand-age through sawtimber stands (table 2), but treatment effect was not significant ($F = 2.37$, $P = 0.146$, d.f. = 3,8). Deer mice were the second most common species, with an average capture rate of 10.0 individuals/100 TN. Capture rates for this species were similar across treatment class except for a lower rate in the seedling stands. No significant differences were found between stand-age class

Table 2.—Average number of individual small mammals captured per 100 trap nights by species, state, and treatment class.

Characteristic	West Virginia				Massachusetts			
	Seedling	Sapling	Sawtimber	Mature	Low deer		High deer	
					Unthinned	Thinned	Unthinned	Thinned
S. red-backed vole (<i>Clethrionomys gapperi</i>) ¹	19.8	12.7	7.3	11.1	15.0	12.3	2.8	3.8
Short-tailed shrew (<i>Blarina brevicauda</i>)	9.1	3.5	3.6	2.1	1.1	1.4	0.2	0.9
E. chipmunk (<i>Tamias striatus</i>)	0.6	0.6	1.2	1.8	0.7	0.4	0.4	1.2
White-footed mouse (<i>Peromyscus leucopus</i>)			0.6		17.2	17.8	30.9	23.4
Deer mouse (<i>P. maniculatus</i>)	7.1	10.0	11.7	11.3				
Woodland jumping mouse (<i>Napaeozapus insignis</i>)	2.1	2.3	0.6	3.0		0.1		
Rock vole (<i>Microtus chrotorrhinus</i>)	1.6	1.4	0.4	1.2				
S. flying squirrel (<i>Glaucomys volans</i>)		1.1	1.4	0.4				
Smoky shrew (<i>Sorex fumeus</i>)	0.2	0.2	0.4					
Meadow vole (<i>M. pennsylvanicus</i>)	1.0							0.1
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	0.7				<0.1			
Masked shrew (<i>S. cinereus</i>)			0.2					<0.1
Long-tailed shrew (<i>S. dispar</i>)			0.2					
Woodland vole (<i>M. pinetorum</i>)		0.2			0.1			0.1
Total all species	42.4	32.1	27.4	31.0	34.2	32.2	34.3	29.4
Total number trap nights ²	497	485	510	508	2036	2055	2021	2008

¹Scientific names from Jones et al. 1975.

²Total number of possible trap nights (WV=540; MA=2160) minus sprung traps.

($F = 0.29$, $P = 0.766$). Short-tailed shrews were the only other species frequently caught in all stand-age classes. Shrews were most common in the seedling stands but no significant treatment effect was found ($F = 0.96$, $P = 0.459$). No significant treatment effect was found for eastern chipmunks ($F = 1.26$, $P = 0.351$), woodland jumping mice ($F = 0.21$, $P = 0.885$), and rock voles ($F = 0.41$, $P = 0.749$), which were caught infrequently in all stand-age classes (table 2). The remaining eight species were caught with less regularity. No further analysis was completed for these species. No significant treatment effect was found in the simultaneous capture rates of the six most commonly trapped species (i.e., red-backed and rock voles, short-tailed shrews, chipmunks, and deer and jumping mice) (Wilks lambda = 0.046, Rao's $F = 0.979$, $P = 0.54$).

Massachusetts

Over 3 years, 2,630 individual small mammals of nine species were captured. Average total capture rate was 32.6 individuals/100 TN. There was a significant decline in capture rate across the years ($F = 30.02$, $P < 0.001$, d.f. = 2,24). The capture rate of 43.7 individuals/100 TN in 1985 declined to 33.7 in 1986 and 20.3 in 1987. The decline was observed across all treatments and all stands.

We found no significant full model treatment effect on total capture rate ($F = 1.78$, $P = 0.204$, d.f. = 3,12). Total capture rate for all species was highest in the unthinned stands and lowest in the thinned stands, especially in the high deer-density stands (table 2). Neither thinning ($F = 3.99$, $P = 0.069$, d.f. = 1,12) nor deer density ($F = 0.60$, $P = 0.453$) had a significant effect on total capture rates.

Species richness was highest in the high deer-thinned treatment class, intermediate in the two low deer-density classes, and lowest in the high deer-unthinned treatment (table

1). White-footed mouse was the most commonly captured species, followed by southern red-backed voles (table 2). Capture rates for both species differed by treatment class ($F = 9.01$, $P = 0.002$, d.f. = 3,12 for mice; $F = 6.06$, $P = 0.009$ for voles), with deer density a significant effect ($F = 20.7$, $P = 0.0007$, d.f. = 1,12 for mice; $F = 17.5$, $P = 0.01$ for voles), and thinning effect nonsignificant ($F = 2.72$, $P = 0.125$ for mice; $F = 0.11$, $P = 0.74$ for voles). Voles were most commonly captured in stands of low deer-density, and mice most commonly captured in stands of high deer-density.

Short-tailed shrews and eastern chipmunks were the only other species captured in each of the four treatments. Shrew captures, like those for red-backed voles, declined with increasing deer density ($F = 6.2$, $P = 0.028$) but showed no significant response to thinning ($F = 3.1$, $P = 0.1$). Chipmunk captures showed no significant response to either deer density ($F = 0.95$, $P = 0.35$) or thinning ($F = 1.52$, $P = 0.24$). The remaining five species were infrequently caught in three or fewer treatment classes, and no further analysis was performed.

Relative capture abundance of the four most commonly captured species (i.e., white-footed mice, red-backed voles, short-tailed shrews, and chipmunks) differed between the two levels of deer density (Wilks lambda = 0.237, Rao's $F = 7.25$, $P = 0.007$). No difference in relative capture abundance was found between the two thinning classes (Wilks lambda = 0.496, Rao's $F = 2.28$, $P = 0.14$).

DISCUSSION

Silvicultural treatments had no significant effect on total small mammal captures. Total capture rates were stable across the range of treatments in both WV (clear-cutting and subsequent regrowth) and MA (intermediate thinning) with the exception of WV seedling stands (table 2). In

those stands, where regenerating trees, shrubs, and herbaceous plants flourish in the sunlight afforded by the removal of the overstory, total capture rates increased. Otherwise, treatment effects on habitat structure were insufficient to alter total capture rates, as changes in the species composition of small mammal captures were compensatory.

Six of the 14 small mammal species captured in WV were captured in all four stand-age classes. Of the other species: red squirrels were observed in all stands but poorly captured in our traps; white-footed mice, woodland and meadow voles, and masked and long-tailed shrews were each captured in one stand; four smoky shrews were captured in three stands; and southern flying squirrels were captured in sapling and older stands. McKeever (1955) generally concurs that these species are uncommon in WV (woodland vole, masked and long-tailed shrew), or are common in forests not sampled in this study (white-footed mouse in lower elevation forests) or other habitats (meadow vole). Smoky shrews and southern flying squirrels are more common WV small mammals but were poorly represented in our sample. Capture data for these species are insufficient for drawing any conclusions regarding species response to clearcutting.

West Virginia red-backed vole and short-tailed shrew captures increased concurrent with a decline in deer mouse captures (table 2). Vole and shrew capture rates were highest in seedling stands. Kirkland (1977) and Lovejoy (1975) reported a similar response in vole captures but not for shrew captures. The increase in vole captures could be a response to the flush in vegetation associated with overstory removal and to the volume of slash occurring immediately subsequent to harvest. These factors alter ground level microclimate, increasing humidity and improving conditions for red-backed voles (Lovejoy 1975, Merritt 1981).

Vole and shrew captures declined and deer mice captures increased as the forest stands matured. Forb cover remained stable with increasing stand-age while fern cover increased and shrub cover declined (table 1). These changes presumably altered microhabitat conditions to the detriment of red-backed voles. In mature forest stands, vole and mouse captures were equal. In these stands, forb cover increased dramatically from conditions observed in sawtimber stands, fern cover declined, and shrub cover remained stable (table 1). These habitat conditions resulted in an increase in red-backed vole captures in mature stands over capture rates for the species in sawtimber stands.

Less frequently trapped rock voles were captured in stands with rock outcrops. Eastern chipmunks captures increased with stand age, and woodland jumping mice captures showed no clear response to stand age. Capture rates for these two species were not related to measured habitat variables (Healy and Brooks 1988).

Species composition of WV small mammal captures and individual species capture rates were not significantly different between treatment classes. No major small mammal species was eliminated by clearcutting and the subsequent maturing of the regeneration of the hardwood stands. These species either survived within clearcut stands or recolonized harvested stands from adjacent uncut stands. Within maturing stands, habitat conditions were sufficiently diverse to support all major species.

These results demonstrate that clearcutting of WV northern hardwood forests allowed for the continued maintenance of the small mammal community. Our data showed the small mammal community to be relatively stable across a silvicultural rotation, with no major changes in composition or capture rates that could alter forest ecosystem functioning or character.

Total capture rates were stable across treatment classes in MA. Treatment effects upon habitat structure in these stands were insufficient to alter total capture rates. However, capture rates for individual small mammal species varied among forest treatments. Deer-density had a greater influence on both individual species capture rates and species composition than did silvicultural treatment. There was a reciprocal change in the relative abundance of red-backed voles and white-footed mice with changes in deer density (table 2).

During the 3 years of this study, fall deer density averaged 18/km² in the high deer-density stands and 3/km² in the low deer-density stands (Healy et al. 1987). Red-backed voles were scarce in high deer-density stands. Ferns and ericaceous shrubs dominated the understory of these stands while the understory of low deer-density stands contained a greater overall number of plant species and forb species were more abundant (Healy et al. 1987). Red-backed voles prefer mesic to hydric sites, especially in the southern portion of their New England range (Miller and Getz 1972, 1973). It seems that foraging by deer may have sufficiently altered the understory vegetation to depress vole populations.

The response of white-footed mice to deer density in MA was less clear. Although capture rates in low deer-density stands were fewer than in high deer-density stands, they nevertheless exceeded capture rates for red-backed voles in all treatment classes (table 2). White-footed mice are ubiquitous in habitat preference within the forest ecosystem (King 1968, Godin 1977, Hamilton and Whitaker 1979). Whereas Wolff and Dueser (1986) suggest that these two species can coexist noncompetitively through microhabitat and food habit differences, our data suggest that mice capture rates are suppressed in stands with high vole capture rates. Our stand data are at too

coarse a scale to address microhabitat separation. One would need to manipulate vole populations experimentally to evaluate whether the abundance of voles is competitively suppressing mice populations in low deer-density stands with better quality vole habitat.

Short-tailed shrews captures were more common in low deer-density stands, a possible response to the greater forb cover observed in these stands and probable increase in ground level humidity. Eastern chipmunk captures offer no ready interpretation in regard to response to treatment effect or habitat structure. The remaining five species were captured so infrequently that it is impossible to draw any conclusions as to the effects of either thinning or deer density on capture rates.

Thinning MA oak forests had no significant effect on capture rates of the four major small mammal species or species composition of the captures. From a management perspective, intermediate thinning of these forests did not alter the continuation of the pretreatment small mammal community. For those situations where white-tailed deer have been allowed to reach population levels where vegetation is altered, significant changes in the small mammal community are found. Silvicultural treatment effects on small mammal habitat are temporary and ecosystem resources (i.e. nutrients, energy) remain available to small mammals. Long-term, high populations of deer, a large, possibly competing herbivore, alter the structure and composition of small mammal habitat to the detriment of some species.

CONCLUSIONS

The small mammal community is an important component of northeastern forested ecosystems, functioning both as a consumer of plant and animal biomass and as prey to numerous predators. Intermediate thinning

and clearcutting treatments, which are common silvicultural practices, have minimal or ephemeral effects on the numbers of small mammals and the composition of the small mammal community found in these forests. Long-term, high deer populations may permanently alter habitat structure to the extent that changes occur in small mammal community composition.

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Habitat Structure and the Distribution of Small Mammals in a Northern Hardwoods Forest¹

Jeffery A. Gore²

In northern temperate forests small mammals are distributed unevenly across available habitat, even within a single forest type or age class (Dueser and Shugart 1978, Vickery 1981, Parren 1981, Seagle 1985a). Differential use of certain segments or microhabitats within a broader habitat type has most often been reported for sympatric species of small mammals, but intraspecific variation in microhabitat use has also been noted (Kitchings and Levy 1981, Vickery 1981, Seagle 1985a).

Differential use of microhabitats by small mammals may be a consequence of the ecological requirements of each species (i.e. habitat selection) or it may be the result of partitioning of habitat by competing species (Crowell and Pimm 1976, Porter and Dueser 1982). Another hypothesis is that the observed use of microhabitats by small mammals is primarily a function of the density of small mammal populations.

Under this hypothesis, use of a certain microhabitat is determined more by the availability of animals to occupy the area than by structural

characteristics of the microhabitat. Extrinsic factors, such as food availability, disease, or predation, could alter population levels and thus indirectly influence the distribution of small mammals among microhabitats. Observed microhabitat use might also be a function of some combination of habitat selection, competitive partitioning, and factors affecting population density.

The question of which mechanism most influences the distribution of small mammals is of more than academic importance. If small mammals select among microhabitats based on structural features, then disturbance such as timber harvesting may have a considerable impact on population density or species composition. Conversely, if the distribution of small mammals is primarily a function of population density, then habitat disturbance is likely to have less effect, or at least a less direct effect, on local populations. Furthermore, if microhabitat requirements are known, it might be possible to manipulate population levels by altering structural components of the habitat.

I measured use of microhabitat by small mammals in an old-growth northern hardwoods (*Acer-Fagus-Betula*) forest, a habitat that contains a variety of microhabitats (Bormann and Likens 1979) and supports several species of small mammals (Lovejoy 1970). In this paper I identify the small mammal-microhabitat associations observed, compare them to re-

Abstract.—The influence of habitat structure on the distribution of small mammals was studied in an old-growth northern hardwoods forest in New Hampshire. Logistic regression equations developed with data from three live-trapping grids were able to classify locations of just three of eight small mammal species better than expected by chance. For all species the regression models failed to correctly predict presence in an independent grid. At the scale tested, habitat structure had little effect on the distribution of small mammals within this forest type.

sults of previous studies, and suggest that the distribution of small mammals among microhabitats in the northern hardwoods forest is influenced little by structural features of the forest.

Methods

The study area was located in the White Mountain National Forest, New Hampshire in a topographically isolated site known as the Bowl (Martin 1977). All fieldwork was confined to the uncut, old-growth northern hardwoods forest that comprises about 210 ha in the lower (600-750 m) elevations of the Bowl. The old-growth forest is structurally heterogeneous; numerous treefalls and gaps in the canopy are present and the portion of the forest floor covered by rock, soil, water, or vegetation varies greatly across the stand (Gore 1986).

Trapping

In 1983, small mammals were live-trapped on three 60 x 105-m grids, each consisting of 40 trapping stations spaced at 15-m intervals along five rows. Two stations were added to each grid in 1984 to increase sampling at seeps and along streams. A fourth grid of 42 trapping stations was also established in 1984. This grid was used to evaluate the robust-

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ness of models of microhabitat use that were developed with data from the initial three grids.

One Sherman (5 x 6 x 17 cm), Pymatuning (Tyron and Snyder 1973), and pitfall trap were located at each trapping station (Gore 1986). Traps were baited with sunflower seeds and set simultaneously for four consecutive days each month from August to October, 1983 and June to October, 1984. Each trapping period began 3-5 days after a new moon (to minimize variation in ambient light) and continued regardless of weather conditions. Captured animals were marked and released at the capture site. In 1983, 4,320 trap-nights (12 nights x 120 stations x 3 traps) were recorded on three grids. In 1984 four grids provided 10,080 trap-nights (20 nights x 168 stations x 3 traps).

Microhabitat

At each trapping station microhabitat was quantified by measures from within the 15 x 15-m plot in which the station was centered. The variables used to quantify the habitat are defined in table 1 and the methods for measuring them are described in detail by Gore (1986).

The 26 habitat variables selected for analysis were a subset of a larger group of variables on which measures were made. The number was reduced in order to facilitate interpretation of results and to increase the ratio of sample cases to variables (Morrison 1985). The initial group was condensed by deleting one of each pair of highly correlated ($r > 0.50$) variables that were similar in ecological form or function. Some highly correlated variables, such as the number of dead trees and the number of logs, were retained because I felt they represented distinct ecological features. Variables were included regardless of whether their means or distributions varied between capture and no-capture stations. This allowed significant linear

combinations of variables to be incorporated, but at the risk of complicating the interpretation of results.

Data Analysis

Chi-square tests (Snedecor and Cochran 1980) were used to identify statistically significant associations between capture locations of all possible pairs of species. Within species, differences between capture locations in different years and seasons were analyzed. The relative strength of associations was measured via the contingency correlation coefficient, Phi (Brown 1983).

Habitat variables from plots with and without captures in 1984 were compared for each small mammal species. Capture locations from the

entire trapping period were grouped even though some values, such as for vegetative cover, varied between seasons. If the habitat values within the two groups were normally distributed and had equal variances, significant differences between groups were determined via t-tests; if not, Mann-Whitney tests were used (Snedecor and Cochran 1980).

Logistic regression (Bishop et al. 1975, Engelman 1983) was used to identify, for each mammal species, the microhabitat variables that accounted for statistically significant portions of the variation in capture success. The product of the analysis is a set of regression equations for predicting presence of each species at a station based upon quantitative measures of the station's habitat characteristics. Logistic regression

Table 1.—Names and definitions of 26 habitat variables measured at each trapping station in 1984.

Name	Definition
SLOPE	angle of ground from horizontal (% of 90)
NTREES	number of trees (stems > 10 cm diameter)
BATREE	basal area (m ²) of trees
DEDTREE	number of dead trees
NSTUMPS	number of stumps (dead trees < 1.5 m high)
TREEDIS	mean distance (m) from trees to station center
NSHRBL3	number of shrubs/saplings (i.e. stems < 10 cm diameter with diameter < 3 cm (measured 10 cm above ground)
NSHRB36	number of shrubs/saplings with diameter 3-6 cm
NSHRBG6	number of shrubs/saplings with diameter 6-10 cm
NLOGS	number of logs (stems > 10 cm diameter)
LOGDIST	mean distance (m) from logs to station center
AVGVOLA	mean volume (m ³) of logs in class of least decay
AVGVOLB	mean volume of logs in class of moderate decay
AVGVOLC	mean volume of logs in class of advanced decay
DVEG	relative cover (%) by vegetation < 0.5 m above ground
CVEG	relative cover by coniferous vegetation < 0.5 m above ground
ROCK	relative cover by rocks > 0.5 m ²
SOIL	relative cover by exposed soil
WATER	relative cover by water
VEG52	relative cover by vegetation 0.5-2 m above ground
CVEG52	relative cover by coniferous vegetation 0.5-2 m
VEGT2	relative cover by vegetation > 2 m above ground
CVEGT2	relative cover by coniferous vegetation > 2 m
AVGLTR	mean depth (cm) of leaf litter
AVGHUMS	mean depth (cm) organic soil (humus)
AVGSHR	mean horizontal sheer strength (kg/m) of soil

was used instead of discriminant analysis because it does not assume that independent or explanatory variables are normally distributed or have homogeneous variances (Press and Wilson 1978).

I used the BMDP-LR computer program (Engelman 1983) to construct regression equations, or models, for predicting microhabitat use as defined by captures. The program selected, in a stepwise manner, habitat variables that distinguished stations where animals were captured from those where they were not. Variables were entered into an equation if their F value was significant at $P < 0.10$ and removed if P subsequently exceeded 0.15.

Initial regression models were formed using data obtained in 1984 from Grids 1-3. The regression models for each mammal species were used to classify stations within the three grids as locations where the species was either present or absent. The models were then used to predict the presence of each species at stations in Grid 4. Finally, new regression models were developed for each species using data from all four grids. These were compared to the models from the initial three grids in order to assess the effect of different sites on the models. The Kappa sta-

tistic (Fleiss 1973, Engelman 1983) determined the significance of agreement between locations where a species was observed and the species-present locations predicted by the regression models.

Results

Trapping

Thirteen species of small mammals were captured during the study, but only those captured more than ten times are considered. The number of captures varied widely among species and, for some species, between years (table 2). The smokey shrew (*Sorex fumeus*), pygmy shrew (*S. hoyi*), and eastern chipmunk (*Tamias striatus*) were captured infrequently in both 1983 and 1984, while the masked shrew (*S. cinereus*) and the southern red-backed vole (*Clethrionomys gapperi*) were common in both years. The northern short-tailed shrew (*Blarina brevicauda*), deer mouse (*Peromyscus maniculatus*) and woodland jumping mouse (*Napaeozapus insignis*) were captured more often in 1984 than in 1983.

Captures from August through October at the 120 stations trapped in both years were compared for each

species to determine whether 1983 and 1984 capture locations were associated. For all but two species, individuals were captured in both years at few (0-8 percent) of the stations with captures. No species showed a significant association in capture locations between years (X^2 tests, $P > 0.05$). Even for deer mice and jumping mice, which were abundant in both years, stations with captures in both years comprised only 32-41 percent of all stations with captures of these species.

A similar comparison was made between the capture locations of each species in summer (June-August) and fall (September-October) of 1984 on all four grids. No species exhibited a significant ($P > 0.05$) association between summer and fall locations.

For all trapping periods and species combined, each trapping station had at least two captures. In 1984, all 168 stations recorded at least one capture and 85 percent had more than four captures. The maximum number of captures at a single station was 22 for all species combined and 15 for a single species, the jumping mouse. Only for deer mice and jumping mice did stations with multiple captures outnumber stations with single captures. All other species were taken only once or not at all at the majority of trapping stations.

The only pairs of species captured at the same locations more often than expected by chance (X^2 tests, $P < 0.05$) were jumping mouse:red-backed vole, short-tailed shrew:masked shrew, and short-tailed shrew:smokey shrew. The association between each pair was positive and weak ($0.15 < \Phi < 0.30$).

Some animals died after capture, but the effect upon local populations of each species was unknown. For abundant species that experienced low mortality, such as the deer mouse and jumping mouse, the effect was probably negligible. For the shrews, which had high mortality rates during capture, the effect may have been substantial. However, cap-

Table 2.—Number of individuals captured, total captures, and individuals captured per 100 trap-nights (TN) for eight small mammal species in 1983 and 1984.

Species	Number of captures					
	1983			1984		
	Indivi- duals	Total	/100 TN	Indivi- duals	Total	/100 TN
Short-tailed Shrew	5	5	0.2	160	170	2.4
Masked Shrew	32	32	1.1	69	73	1.0
Smokey shrew	3	3	0.1	8	9	0.1
Pygmy shrew	6	6	0.2	4	4	<0.1
Eastern chipmunk	6	7	0.2	22	26	0.3
Deer mouse	41	61	1.4	303	571	4.5
Red-backed vole	25	30	0.9	64	87	1.0
Jumping mouse	71	92	2.5	305	494	4.5

ture rates indicated no adverse effects on shrew abundance. In 1984 more shrews of each species were captured in September than in the previous three months. Furthermore, of the four shrew species, only captures of pygmy shrews declined between years (table 2).

Microhabitat Use

Differences between habitat values for the capture and no-capture stations of Grids 1-3 from 1984 were compared. For each species, at least one habitat variable differed significantly between stations with and without captures (table 3).

Logistic regression is not useful if the number of cases of either of the dependent variable values (species presence or absence) is less than five percent of the total number of cases (D. Hosmer, University of Massachusetts, personal communication). Because the pygmy shrew was found at only two percent of the stations, it was deleted from the analysis. Deer mice and smokey shrews each also had widely disparate group sizes, 95 percent present and 95 percent absent respectively; therefore, results for these species should be considered cautiously.

The first set of logistic regression models of microhabitat use were based on captures in 1984 from the 126 stations in Grids 1-3. The number of significant variables included in each model ranged from one, when presence of red-backed voles was the dependent variable, to 12, when presence of eastern chipmunks was used (table 4). For most species the variables included in the regression models were not the same as those whose means differed between capture and no-capture stations (table 3). This suggests that some linear combination of habitat variables was important in defining the microhabitat where a species was captured, even though individual variables alone were not.

The habitat variables included in the logistic regression models (table 4) were selected because each was associated with a significant ($P < 0.10$) portion of the variance in the capture data of a species. However, if these variables and their regression coefficients cannot be used to correctly predict the capture success of a species at a station, they are of limited practical value regardless of their statistical significance. To assess the utility of regression models as descriptors of microhabitat, they were independently used to classify each trapping station, based on habitat parameters, as one with the species present or absent (table 5).

Tests of the agreement between predicted and observed capture success were not possible for the smokey shrew because no sites were classified as having the species present. The regression model was not able to identify, based upon the habitat variables measured, the eight sta-

tions that captured smokey shrews. Conversely, nearly all stations were predicted to capture deer mice and jumping mice (table 5). The regression models for those two species were unable to distinguish those stations where the animals were not captured.

For the other four species the numbers of stations with and without captures were more similar and, consequently, so were the number of species-present and species-absent classifications. For red-backed voles, however, only 47 percent of the classifications of present were correct and this was not significantly better than chance (table 5). Only for the eastern chipmunk, short-tailed shrew, and masked shrew were the regression models able to classify capture success at a level better than chance agreement. For these three species, the logistic regression models may be useful descriptors of the microhabitat used within Grids 1-3.

Table 3.—Means (SE) of habitat variables that differed significantly between stations with and without captures of each species in Grids 1-3 in 1984.

Species	Habitat Variable ¹	Stations with captures	Stations without captures	P ²
Short-tailed shrew	NSHRBL3	188 (10)	158 (15)	<0.05
	CVEGT2	0.2 (0.1)	0.0	<0.05
	VEG52	30.9 (2.0)	24.7 (2.2)	<0.05
Masked shrew	LOGDIST	5.1 (0.1)	5.5 (0.1)	<0.05
	AVGVOLA	0.20 (0.06)	0.06 (0.02)	<0.001
	DVEG	38.2 (2.4)	27.6 (1.3)	<0.001
	AVGLTR	3.4 (0.1)	3.0 (0.1)	<0.05
Smokey shrew	DEDTREE	0.63 (0.12)	1.0 (0.1)	<0.05
	AVGLTR	3.8 (0.3)	3.1 (0.1)	<0.05
Eastern chipmunk	BATREE	0.93 (0.08)	0.77 (0.02)	<0.05
	AVGVOLA	0.23 (0.10)	0.08 (0.02)	<0.05
	VEG52	37.1 (4.5)	26.9 (1.6)	<0.05
Deer mouse	NSHRBL3	220 (28)	168 (9)	<0.05
	DEDTREE	0.85 (0.0)	1.6 (0.42)	<0.05
	NSHRBG6	7.8 (0.4)	10.8 (1.2)	<0.05
	AVGVOLB	0.23 (0.03)	0.51 (0.14)	<0.05
Red-backed vole	DVEG	36.9 (2.3)	27.7 (1.4)	<0.001
Jumping mouse	VEGT2	75.4 (0.9)	70.2 (2.6)	<0.05

¹Definitions of habitat variables are given in table 1.

²Probability that capture groups have equal means.

Because of the large number of variables included in the regression model for the eastern chipmunk (table 4), it was difficult to concisely describe the microhabitat of this species. Briefly, the eastern chipmunk was associated with large trees (+BATREE), downed wood (+NLOGS, -LOGDIST, +AVGVOLB, +AVGVOLC), and dense vegetation taller than 0.5 m (+VEG52, +VEGT2, +NSHRB36).

The microhabitat of the short-tailed shrew has fewer variables but is also difficult to characterize. Captures were negatively associated with

numbers of medium-sized shrubs and with vegetative cover between 0.5 and 2 m above ground. The masked shrew was found at stations with numerous logs and dense vegetation <0.5 m tall. The positive association with slightly decayed logs and dense ground cover and the negative association with standing dead trees suggest that recent treefalls may provide good habitat for masked shrews.

To be useful predictors of species microhabitat, regression models should be successful with data that are independent of those from which

the models were formed. To test site-specificity of regression models, they were applied to data from 42 stations in Grid 4. Unlike the other three grids, Grid 4 had a perennial stream running through it, two extensive canopy gaps from recent treefalls, and highly variable soil conditions.

Regression models from each of the seven species were used to classify the stations in Grid 4 according to capture success. None of the classifications, even those of the eastern chipmunk, short-tailed shrew, and masked shrew were correct more often than expected due to chance (for all tests Kappa <0.48, P>0.05).

Because none of the regression models were useful in predicting capture locations in Grid 4, data from all four grids were combined and new logistic regression models for predicting species presence were developed to determine the influence of data from Grid 4 (table 7). Deer mice, jumping mice, and smokey shrews again had widely disparate group sizes and the models could not correctly classify the stations in the less common group (table 7).

Agreement between observed and predicted locations was significant for red-backed voles as well as eastern chipmunks, short-tailed shrews, and masked shrews (table 7), which had significant models earlier. Some of the variables included in the models of each species (table 6) were different from those included when only data from Grids 1-3 were used (table 4). For the masked shrew, eastern chipmunk, and red-backed vole the regression models created with and without the data from Grid 4 were similar, even though the predictions from Grids 1-3 for the red-backed vole were not better than expected by chance. The coefficients changed but most variables were the same. This suggests that for these three species the microhabitats in Grid 4 were similar to those identified in the other three grids. The relationship of species to microhabitat parameters may not be as sensitive

Table 4.—Logistic regression models for predicting presence of small mammal species based on data collected in Grids 1-3 in 1984.

Species	Independent Variable ¹	Regression Coefficient	Coefficient/Standard Error
Short-tailed shrew	NSHRB36	-0.062	-1.784
	VEG52	-0.053	2.059
	CONSTANT	0.487	0.907
Masked shrew	DEDTREE	-0.704	-2.538
	LOGDIST	-0.660	-2.577
	AVGVOLA	2.621	2.212
	DVEG	0.137	3.273
	CONSTANT	0.784	0.566
	AVGLTR	1.514	2.631
Smokey shrew	CONSTANT	-7.869	-3.651
	NTREES	-0.210	-1.431
Eastern chipmunk	BATREE	2.523	1.957
	NSHRB36	0.123	1.457
	NSHRBG6	-0.447	-2.831
	NLOGS	0.188	2.171
	LOGDIST	-0.702	-1.651
	NSTUMPS	-1.706	-1.272
	AVGVOLB	3.031	2.584
	AVGVOLC	2.305	2.560
	VEG52	0.052	1.187
	VEGT2	0.086	1.772
	AVGSHR	-0.102	-2.369
	CONSTANT	-3.238	-0.965
	NLOGS	-0.132	-2.033
Deer mouse	AVGVOLB	-1.155	-1.586
	CONSTANT	4.543	4.804
	DVEG	0.112	3.230
Red-backed vole	CONSTANT	-2.450	-4.415
	CVEG52	-0.512	-1.833
Jumping mouse	VEGT2	0.070	2.120
	CONSTANT	-2.544	-1.205

¹See table 1 for definition of habitat variables.

as the regression models suggest. This would account for the poor performance of the models from Grids 1-3 in predicting captures on Grid 4.

For short-tailed shrews the regression model changed greatly when data from Grid 4 were included. Four new variables were added, and the sign of the coefficient was reversed on the only variable, vegetation between 0.5 and 2 m, that was retained. This suggests that captures of short-tailed shrews or the measured habitat parameters poorly reflect the microhabitat requirements of the species, or that short-tailed shrews are not restricted by microhabitat within this forest.

Discussion

In an environment of limited resources, sympatric species are expected to partition resources as a means of coexisting, i.e. avoiding competitive exclusion (Schoener 1974). Since Brown (1973) first suggested that temperate forest rodents would be likely to partition habitat rather than seasonally variable food supplies, numerous studies in northern temperate forests have identified statistically significant associations between habitat structure and small mammal distributions (Dueser and Shugart 1978, Kitchings and Levy 1981, Parren 1981, Vickery 1981, Schloyer 1983, Seagle 1985a).

Statistical significance, however, does not necessarily impart biological meaning to observed patterns of species distributions. Few authors have tested the biological relevance of their models of microhabitat use by using them to predict microhabitat use at independent locations or times. Parren and Capen (1985) found that capture locations of deer mice could not be accurately predicted using discriminant functions of microhabitat use developed with data from similar habitats the previous year. Similarly, none of the logistic regression models I developed

were useful in predicting capture locations at stations other than those from which the models were developed.

One reason for the poor predictive capabilities of the multivariate models may be that trapping does not accurately portray the relationship between species presence and habitat requirements. In addition, the way in which habitat features are measured may not depict the variability perceived by small mammals or the variation in microhabitat structure may be small relative to the niche breadth of each species. Unfortunately, these problems are not easily identified or solved. Ideally, the activity of many individual animals would be intensively monitored, but that is very difficult to accomplish.

Another reason for the poor performance of the models is that problems in applying the multivariate analyses, such as disparate sizes of presence and absence groups and multicollinearity of variables, make it difficult to interpret the results of habitat models (Noon 1984). The scale at which habitat and small mammals are sampled also greatly

affects the relationship that can be defined (Morris 1984).

Despite these potential limitations, I believe the inability of my models to predict species presence on a independent grid in the same forest stand suggests that structural features alone, at least at the microhabitat level, are not important to the distribution of small mammals. Comparisons of capture locations and review of habitat requirements for each species supports my argument.

The locations where species were captured suggest that no interspecific segregation of microhabitats occurred. Overlap in capture sites was high among species and no inverse relationships were observed, even when data were examined by season. This suggests that habitat partitioning or microhabitat selection is absent or operating at a finer scale than my trap stations.

The weak association I found among capture locations of each species between years and seasons suggests that individual species were not selecting particular trapping stations. It is possible that subtle shifts in the microhabitat used would not be per-

Table 5.—Classification of 126 trapping stations in Grids 1-3 as locations where each of eight small mammal species is present or absent based on logistic regression models, and agreement between predicted and observed classifications.

Species	No. of stations classified ¹		% Correct ²		Agreement ³		
	Present	Absent	Present	Absent	K	ASE	P
Short-tailed shrew	104	22	64	64	0.185	0.079	<0.025
Masked shrew	23	103	65	81	0.381	0.093	<0.001
Smokey shrew	0	126	0	94	—	—	—
Eastern chipmunk	12	114	75	92	0.548	0.114	<0.001
Deer mouse	125	1	94	0	0.014	0.013	NS
Red-backed vole	15	111	47	72	0.113	0.084	NS
Jumping mouse	124	2	87	50	0.079	0.090	NS

¹Prior probability of presence = 0.05.

²Percent of stations where present/absent classification agreed with observations from trapping in 1984.

³K = Kappa statistic (Fleiss 1973). ASE = asymptotic standard error. P = Probability that agreement is due to chance, i.e. K=0. NS = not significant, >0.05.

ceived by examination of trapping locations alone. The microhabitat occupied by small mammals has been reported to shift with season (Kitchings and Levy 1981, Vickery 1981), population density (M'Closkey 1981, Adler 1985), and species composition (Seagle 1985b). This suggests that microhabitat use is dynamic, regardless of whether the shifting is deterministic or stochastic.

Another argument against differential use of microhabitats by the small mammals I observed is the variety of habitats they occupy. The

eight species I found in the old-growth northern hardwoods forest have been found in other age- and size-classes of northern hardwoods forests as well as in other forest types (Lovejoy 1970, Richens 1974, Kirkland 1977, Miller and Getz 1977, Hill 1981, and others). Except for smokey shrews and pygmy shrews, the species are common in a variety of habitats comprising a wide range of structural characteristics. In fact, descriptions of the important habitat features associated with each species do not always agree [e.g. see Hamil-

ton (1941), Brower and Cade (1966), Lovejoy (1970), Vickery (1981), and Parren (1981) for descriptions of jumping mouse habitat]. If each species is common under a wide range of habitat conditions, it seems unlikely that they would partition or select habitat based on the advantages of structural features alone.

Fine discrimination of the forest habitat seems more improbable when the temporal variability of microhabitats is considered. Within the northern hardwoods forest of New Hampshire microhabitats are greatly modified in winter by deep snow cover, in summer by closed canopies and sparse ground cover, and in fall by deep leaf litter. Therefore, resident species must accommodate seasonally variable microhabitats as well as seasonally variable food supplies. The reasoning Brown (1973) used to suggest that temperate forest rodents could not specialize on seasonally variable food resources seems applicable also to seasonally variable microhabitats.

In the forest I sampled, presence of most species at individual trapping stations could not be accurately predicted based on structural features of the habitat. If microhabitat structure does not greatly influence the distribution of small mammals within this forest type, disturbance of the habitat should not directly affect population levels. However, the scale at which the disturbance occurs may determine to what extent local populations are affected. Small scale disturbance of the habitat, such as harvesting by single-tree or small-group selection, would likely not affect species composition or density of the resident small mammals. More wide scale disturbance, such as clear-cutting of the entire forest stand, might alter the habitat so greatly that species abundance and distribution is affected (Kirkland 1977). Given the apparent wide range of habitat conditions in which these small mammals occur, even a large scale disturbance of the northern hardwoods

Table 6.—Logistic regression models for predicting presence of small mammal species based on data collected in Grlds 1-4 in 1984.

Species	Independent Variable ¹	Regression Coefficient	Coefficient/Standard Error
Short-tailed shrew	DEDTREE	-0.355	-2.157
	DVEG	0.053	2.275
	ROCK	0.207	2.721
	VEG52	0.043	1.826
	AVGLTR	0.809	-3.198
	CONSTANT	-3.463	-3.392
Masked shrew	DEDTREE	-0.401	-2.029
	LOGDIST	-0.810	-3.415
	DVEG	0.159	5.348
	AVGHUMS	0.499	2.467
	CONSTANT	-0.475	-0.336
Eastern chipmunk	NSHRBG6	-0.280	-2.825
	NLOGS	0.125	1.979
	NSTUMPS	-1.761	-1.639
	AVGVOLB	2.085	2.762
	AVGVOLC	1.042	1.874
	VEGT2	0.072	2.088
	AVGLTR	0.675	1.867
	CONSTANT	-9.267	-3.506
Deer mouse	DEDTREE	-0.934	-2.511
	NSHRB36	-0.170	-2.366
	AVGVOLB	-1.064	-1.599
	AVGHUMS	-0.794	-2.165
	CONSTANT	9.763	4.248
Red-backed vole	DEDTREE	-0.321	-1.849
	DVEG	0.083	3.778
	CONSTANT	-1.841	-4.365
Jumping mouse	LOGDIST	0.475	1.742
	AVGVOLB	-0.869	-1.815
	SOIL	-0.192	-2.351
	CONSTANT	-0.140	-0.098

¹See table 1 for definition of habitat variables.

forest would likely cause only temporary changes in species composition or population levels of small mammals.

The relationship between small mammals and habitat structure within the northern hardwoods forest remains poorly understood. However, the data presented here, as well as comparisons at different scales (Morris 1984, 1987), suggest that microhabitat features play only a minor role in the distribution of small mammals within the forest. A more important determinant of small mammal distribution may be population size and the factors that affect it, such as food, weather, and predators. Consequently, models for predicting the distribution of small mammals within the northern hardwoods forest will likely remain unsuccessful until factors that affect population size are included. The temporal and spatial scales at which these factors influence distribution must also be addressed.

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Table 7.—Classification of 168 trapping stations in Grids 1-4 as locations where each of seven small mammal species is present or absent based on logistic regression models, and agreement between predicted and observed classifications.

Species	No. of stations classified ¹		% Correct ²		Agreement ³		
	Present	Absent	Present	Absent	K	ASE	P
Short-tailed shrew	106	62	71	68	0.371	0.072	<0.001
Masked shrew	45	123	67	78	0.412	0.075	<0.001
Smokey shrew	2	166	100	96	0.351	0.183	NS
Eastern chipmunk	7	161	71	90	0.314	0.116	<0.01
Deer mouse	167	1	95	0	0.011	0.010	NS
Red-backed vole	27	141	57	72	0.223	0.076	<0.01
Jumping mouse	165	3	88	62	0.133	0.093	NS

¹Prior probability of presence = 0.05.

²Percent of stations where present/absent classification agreed with observations from trapping in 1984.

³K = Kappa statistic (Fleiss 1973). ASE = asymptotic standard error. P = Probability that agreement is due to chance, i.e. K=0. NS = not significant.

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The Value of Rocky Mountain Juniper (*Juniperus scopulorum*) Woodlands in South Dakota as Small Mammal Habitat¹

Carolyn Hull Sieg²

Native woodlands constitute only a small percentage of the total land area in the Northern Great Plains, yet they provide critical habitat for many wildlife species. Isolated woodlands provide a sharp contrast with adjacent grasslands, increasing available cover, vertical structure, and habitat interspersions, and, hence, the number of potential niches available for wildlife. Research on the value of native woodlands as wildlife habitat has focused mainly on wildlife use of deciduous woodlands (Faanes 1984, Gaines and Kohn 1982, Hopkins et al. 1986, Uresk 1982), although the importance of Rocky Mountain juniper woodlands for mule deer (*Odocoileus hemionus*) has been documented (Severson 1981, Severson and Carter 1978). Information on small mammals associated with Rocky Mountain juniper stands is limited to brief studies conducted in North Dakota (Hansen et al. 1980, Hopkins 1983, Seabloom et al. 1978).

Native woodlands in the Northern Great Plains are limited to areas of increased moisture, such as along streams and rivers, and to areas with

increased topographic variation. Rocky Mountain juniper is restricted to areas of steep topography, such as the "Badlands" of North and South Dakota, the Black Hills, areas along drainageways of major rivers, and areas on high limestone plateaus in South Dakota and Wyoming. It is more likely to occur on steep, north-facing slopes, and is often associated with soils that are calcareous, poorly developed, and shallow (Fowells 1965).

The purpose of this study was to characterize small mammal species composition and distribution in Rocky Mountain juniper woodlands and in adjacent mixed-grass rangelands in the Badlands National Park, southwestern South Dakota. The objectives were to determine if the presence of isolated juniper woodlands increased mammal species richness of the area, and to form preliminary hypotheses as to how these woodlands function as small mammal habitat.

Study Area and Methods

The study area is in Pennington County, South Dakota, approximately 15 km south of the town of Wall, in Sage Creek Basin, Badlands National Park. Elevation ranges from 950 to 1000 m above sea level. Annual precipitation averages 36 cm, most of which is received in May, June, and July. The terrain in Bad-

Abstract.—Small mammals and vegetation were sampled over two years in Rocky Mountain juniper woodlands and adjacent grasslands in South Dakota. Juniper woodlands provided specialized habitat for two woodland species, white-footed mice and bushy-tailed woodrats, and attracted a number of species generally associated with grasslands.

lands National Park is typically rough and irregular, with steep bluffs rising above floodplains onto upland grasslands. Dense stands of Rocky Mountain juniper occur on steep, north-facing slopes and in draws. Upland grasslands are dominated by western wheatgrass (*Agropyron smithii*), green needlegrass (*Stipa viridula*), buffalograss (*Buchloe dactyloides*), and blue grama (*Bouteloua gracilis*).

Eight study sites were established, four in Rocky Mountain juniper woodlands on north-facing slopes in draws, and four on adjacent grasslands. Vegetation and relative abundance of small mammals were sampled on a regular basis for 2 years. Plant canopy cover on grasslands and understory cover in the juniper woodlands were sampled in June and August of both sampling years. Plant canopy cover, by species, was estimated in 150, 0.1-m² quadrats spaced at 1-m intervals along three permanent 50-m transects on each site (Daubenmire 1959). Overstory vegetation in Rocky Mountain juniper study sites was sampled in eight, 7- by 7-m macroplots spaced at 30-m intervals on each site. Tree densities, heights, diameters (d.b.h.), and crown heights of all trees were measured.

Small mammal abundance was sampled monthly from June through October in both years. Forty Sherman live traps, spaced at 10-m intervals along two permanent 200-m

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transects, were set on each study site for four consecutive nights, after one night of prebaiting. Total trap effort was 6400 trap nights per vegetation type per year. Rolled oats mixed

with peanut butter were used as bait. Captured animals were identified by species and assigned a unique 4-digit number by toe clipping (Taber and Cowan 1971).

Table 1.—Two-year average percent (\pm SD) canopy cover of dominant species in four Rocky Mountain juniper woodlands and four grassland sites, Badlands National Park, South Dakota.

Category	Juniper	Grassland
Total cover	24.5 \pm 5.5	52.8 \pm 4.9
Litter cover	44.6 \pm 11.3	39.5 \pm 10.2
Bareground	36.7 \pm 11.8	15.8 \pm 8.3
Forbs		
Yellow sweetclover (<i>Melilotus officinalis</i>)	8.7 \pm 4.9	1.2 \pm 1.0
Russian thistle (<i>Salsola kali</i>)	< 1 \pm < 1	2.4 \pm 2.8
Scarlet globemallow (<i>Sphaeralcea coccinea</i>)	< 1 \pm < 1	2.9 \pm 1.8
Grasses		
Western wheatgrass (<i>Agropyron smithii</i>)	1.4 \pm 1.4	9.7 \pm 7.5
Blue grama (<i>Bouteloua gracilis</i>)	< 1 \pm < 1	5.4 \pm 4.0
Cheatgrass (<i>Bromus tectorum</i>)	< 1 \pm < 1	2.5 \pm 1.5
Buffalograss (<i>Buchloe dactyloides</i>)	< 1 \pm < 1	3.4 \pm 3.5
Threadleaf sedge (<i>Carex filifolia</i>)	1.3 \pm 2.1	3.3 \pm 4.2
Sun sedge (<i>Carex heliophila</i>)	< 1 \pm < 1	3.0 \pm 1.5
Stonyhills muhly (<i>Muhlenbergia cuspidata</i>)	3.4 \pm 3.2	0
Littleseed ricegrass (<i>Oryzopsis micrantha</i>)	1.5 \pm 1.4	0
Needleandthread grass (<i>Stipa comata</i>)	< 1 \pm < 1	6.5 \pm 9.0

Table 2.—Two-year average number (\pm SD) of small mammals captured per site in four Rocky Mountain juniper woodlands and four adjacent grassland sites, Badlands National Park, South Dakota.

Species	Juniper	Grassland
Meadow vole (<i>Microtus pennsylvanicus</i>)	< 1 \pm 1.1 ^a	14.8 \pm 17.2 ^b
House mouse (<i>Mus musculus</i>)	< 1 \pm 0.4 ^a	0 ^a
Bushy-tailed woodrat (<i>Neotoma cinerea</i>)	1.0 \pm 1.2 ^a	0 ^a
Northern grasshopper mouse (<i>Onychomys leucogaster</i>)	1.0 \pm 1.1 ^a	4.9 \pm 3.3 ^b
Plains pocket mouse (<i>Perognathus flavescens</i>)	1.0 \pm 1.8 ^a	1.0 \pm 1.8 ^a
Hispid pocket mouse (<i>Perognathus hispidus</i>)	1.0 \pm 0.9 ^a	2.1 \pm 2.0 ^a
White-footed mouse (<i>Peromyscus leucopus</i>)	20.4 \pm 12.7 ^b	1.6 \pm 2.2 ^a
Deer mouse (<i>Peromyscus maniculatus</i>)	44.5 \pm 24.9 ^a	35.9 \pm 27.4 ^a
Western harvest mouse (<i>Reithrodontomys megalotis</i>)	< 1 \pm 1 ^a	2.9 \pm 3.5 ^b
Thirteen-lined ground squirrel (<i>Spermophilus tridecemlineatus</i>)	< 1 \pm 1 ^a	11.0 \pm 6.9 ^b
Total	68.5 \pm 27.4 ^a	74.1 \pm 21.9 ^a

^aMeans in a row followed by the same superscript were not significantly ($P > 0.1$) different.

Differences in small mammal numbers and vegetation between the two vegetation types were tested with repeated measures analyses of variance (SPSS 1986). Both years were combined for analyses. Total unique small mammals and numbers of each species were analyzed separately: trap session and year were within-subject factors; vegetation type was the between-subject factor. Total plant canopy cover was the vegetation parameter analyzed: sampling session and year were within-subject factors; vegetation type was the between-subject factor. Homogeneity of variances was tested with Bartlett's Box F test; variables with heterogeneous variances were log-transformed.

Results

Vegetation

Overstory vegetation in juniper woodlands was nearly a monoculture of Rocky Mountain juniper, although an occasional green ash (*Fraxinus pennsylvanica*) tree was observed. Tree density averaged 260 trees/ha (\pm 117 SD), and ranged from an average of 160 to 380 trees/ha on the four sites. Tree heights ranged from a mean of 2.8 to 3.1 m, and the crowns extended nearly to the ground, averaging approximately 2.3 m in height. The diameters of the juniper trees were small, ranging from a mean of 4.8 cm to 7.6 cm.

Total plant canopy cover of understory vegetation in the juniper woodlands was lower ($P < 0.01$) than on grasslands. Total cover in the juniper woodlands averaged 25% (table 1). Yellow sweetclover (*Melilotus officinalis*) was the most common understory plant, then stonyhills muhly (*Muhlenbergia cuspidata*) and littleseed ricegrass (*Oryzopsis micrantha*). Shrubs were uncommon in juniper woodlands; chokecherry (*Prunus virginiana*), western wild rose (*Rosa woodsii*), western snowberry (*Sym-*

phoricarpos occidentalis), and skunkbush sumac (*Rhus aromatica*) each comprised less than 1% of the total canopy cover. Litter cover in the juniper woodlands averaged 45% and bare ground 30%.

Total plant canopy cover on grasslands averaged 53% (table 1). Western wheatgrass was the most common plant species, then needleandthread grass (*Stipa comata*), blue grama, and buffalograss. Scarlet globemallow (*Sphaeralcea coccinea*) was the most common forb. Shrub species were limited to fringed sage (*Artemisia frigida*) and dwarf sagebrush (*A. cana*), each comprising a small percentage of the total cover on grasslands. Mean litter cover was 40% and bare ground 16% over the two sampling years.

Small Mammals

Average numbers of small mammals were similar ($P = 0.4$) on the two vegetation types; however, species composition differed between juniper woodlands and adjacent grasslands (table 2). Deer mice (*Peromyscus maniculatus*) were the most common species captured in both juniper woodlands and on grasslands, constituting 66% of the total capture in juniper woodlands and 48% on grasslands. Number of deer mice captured was similar ($P = 0.4$) in both vegetation types, averaging 42 and 36 individuals per site in juniper woodlands and grasslands, respectively. White-footed mice (*P. leucopus*) were the next most abundant small mammal species captured in juniper woodlands, constituting approximately 29% of the total captures; their numbers were much lower ($P = 0.04$) on grassland sites. Bushy-tailed woodrats (*Neotoma cinerea*) were captured in small numbers in the juniper woodlands but were absent from grasslands. Average numbers of meadow voles (*Microtus pennsylvanicus*) ($P = 0.03$), thirteen-lined ground squirrels (*Spermophilus*

tridecemlineatus) ($P = 0.03$), northern grasshopper mice (*Onychomys leucogaster*) ($P = 0.06$), and western harvest mice (*Reithrodontomys megalotis*) ($P = 0.08$) were higher on grasslands than in juniper woodlands. Small numbers of plains pocket mice (*Perognathus flavescens*) and hispid pocket mice (*P. hispidus*) were captured in both vegetation types. One house mouse (*Mus musculus*) was captured in a juniper woodland.

Discussion

Rocky Mountain juniper stands did not support significantly higher numbers of small mammals than did adjacent grasslands, but enhanced small mammal diversity by providing specialized habitat for white-footed mice and bushy-tailed woodrats. White-footed mice prefer and are commonly restricted to riparian forests and shrubby habitats in this region (Armstrong 1972, Seabloom et al. 1978), and were a common species in Rocky Mountain juniper woodlands in North Dakota (Hopkins 1983). White-footed mice forage (M'Closkey 1975) and nest (Wolff and Hurlbutt 1982) in trees and show a tendency to use woody vegetation as escape routes (Barry and Francq 1980). Their preferred habitat is often characterized by dense woody understory (Yahner 1982). Rocky Mountain juniper woodlands lack vertical layering provided by shrubs, but the dense tree canopy and presence of branches nearly to the ground may substitute for shrub layers found in other woodlands. Further, juniper woodlands may function as dispersal pathways for woodland species such as white-footed mice. Turner (1974) postulated that riparian habitats along major drainageways allowed the western expansion of the white-footed mouse.

Bushy-tailed woodrats are often restricted to rocky areas in this region (Jones et al. 1983), and their

presence has been documented in deciduous woodlands in northwestern South Dakota (Hodorff et al. In Press). Bushy-tailed woodrats were captured in ponderosa pine (*Pinus ponderosa*) stands, toe slopes, hilly scoria, and upland breaks in western North Dakota (Seabloom et al. 1978). Juniper stands likely provide den sites, which grasslands lacked. Middens constructed of juniper branches were observed in three of four Rocky Mountain juniper sites in this study.

Three species—deer mice, plains pocket mice, and hispid pocket mice—apparently showed no preference between grasslands or juniper woodlands. The high proportion of deer mice in the total capture on both grasslands and in juniper woodlands is not uncommon on the Northern Great Plains. Deer mice are a ubiquitous species, occurring in nearly every habitat in this region (Jones et al. 1983). Deer mice were the most commonly captured species in green ash woodlands in northwestern South Dakota (Hodorff et al. In Press), and were abundant in both green ash and Rocky Mountain juniper woodlands in western North Dakota (Hopkins 1983). Rocky Mountain juniper woodlands in South Dakota are probably not critical habitat for deer mice, but when available, will be exploited by this adaptive species.

Hispid pocket mice apparently prefer rocky areas, where a variety of shrubs, forbs, and yucca (*Yucca* spp.) grow (Jones et al. 1983). Plains pocket mice are considered rare mammals in South Dakota (Houtcooper et al. 1985); hence little is known about the distribution and habitat preferences of this species in the state. Hodorff et al. (In Press) captured low numbers of both plains and hispid pocket mice in green ash woodlands in northwestern South Dakota. Haufler and Nagy (1984) captured plains pocket mice in pinyon pine (*Pinus edulis*)-Utah juniper (*J. osteosperma*) woodlands in Colorado, and reported that juniper comprised 17% of the pocket mouse's diet. The small captures of

both species of pocket mice make generalizations about habitat preference suspect, but Rocky Mountain juniper woodlands likely provided habitat interspersed and food resources for these species.

Juniper woodlands, with sparse understory cover, are atypical habitat for grassland inhabitants such as meadow voles, thirteen-lined ground squirrels, northern grasshopper mice, and western harvest mice. Meadow voles, in particular, are generally associated with dense stands of grass (Birney et al. 1976). However, Rocky Mountain juniper woodlands in southwestern North Dakota supported meadow voles in some areas (Seabloom et al. 1978) and prairie voles (*M. ochrogaster*) on other sites (Hopkins 1983).

The ability of North Dakota juniper woodlands to support microtines was attributed to differences in plant community attributes. Littleseed ricegrass and mosses dominated the understory and total plant cover averaged over 60% (vs. 25% in South Dakota) in most juniper stands sampled by Hopkins (1983) (Hansen et al. 1984). The more dense understory of the North Dakota woodlands, which South Dakota woodlands lacked, apparently provided adequate cover for microtines.

Thirteen-lined ground squirrels were most frequently captured in northwestern South Dakota in roadways and fencerows in shortgrass prairies (Andersen and Jones 1971). Northern grasshopper mice are generally restricted to shortgrass and desert sites (McCarty 1978), in areas with adequate dust-bathing sites (Egoscue 1960). Western harvest mice were occasionally captured in pinyon-juniper woodlands in southeastern Colorado, but were associated with dense herbaceous cover lacking tree canopy cover (Ribble and Samson 1987). Rocky Mountain juniper woodlands may provide supplemental food resources for small mammals generally restricted to grasslands.

Conclusion

Rocky Mountain juniper woodlands enhance small mammal richness of the generally treeless Northern Great Plains by providing specialized habitat for at least two species, bushy-tailed woodrats and white-footed mice. Juniper woodlands lack well-developed shrub layers, but the dense canopy of the juniper trees and crowns that extend nearly to the ground may provide foraging and nesting substrates for woodland mammals. Further, Rocky Mountain juniper woodlands may function as dispersal pathways for these two species. Juniper woodlands lack dense herbaceous understories necessary to support microtines such as meadow voles, but likely serve as food resource supplemental areas for a variety of mammals associated with grasslands. Adaptable species such as the deer mouse may not require juniper woodlands, but will exploit this habitat when available. Finally, Rocky Mountain juniper woodlands may figure into the habitat needs of pocket mice, but low captures of two species preclude clear definition of preferred habitat.

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Postfire Rodent Succession Following Prescribed Fire In Southern California Chaparral¹

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The chaparral community of southern California is associated with nearly two million years of fire history (Hanes 1971). In recent centuries major fires have occurred at intervals of 20 to 40 years (Byrne et al. 1977; Philpot 1977). Postfire plant succession (Patric and Hanes 1964, Hanes and Jones 1967, Hanes 1971) and the fire itself have varying short term effects on the birds and small mammals found in the chaparral (Lawrence 1966, Quinn 1979, Wirtz 1977, 1979). Wirtz (1977) summarized the work of earlier authors concerning conditions in small vertebrate microhabitats during fire, vertebrate behavior during fire, and survival of small vertebrates exposed to fire. Both Lawrence (1966) and Quinn (1979) studied rodent populations before and after a burn, in addition to documenting microhabitat conditions during the fire. Wirtz (1977,

1982, 1984) presents preliminary analyses of data collected on postfire rodent succession following wildfire in the chaparral community of southern California.

Because of the recently recognized significance of the use of prescribed fire in the management of chaparral ecosystems, the Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, began formulating plans in 1983 for a series of prescribed fires in the San Dimas Experimental Forest, located in the San Gabriel Mountains of southern California, that might be utilized for long range studies of the effects of prescribed fire in chaparral. In October, 1984, the Forest Service burned four chaparral watersheds of approximately 40 ha each in the San Dimas Experimental Forest. This paper describes the changes in rodent community structure for the 4-year period following prescribed burning.

Methods

In October, 1984, four chaparral watersheds of approximately 40 ha each were subjected to prescribed burns in the San Dimas Experimental Forest. The vegetation of the two of these watersheds (874 and 775) had been hand cut in the spring of 1984 to produce the dried fuel for an exceptionally hot fire. Two adjacent watersheds (804 and 776) burned normally

Abstract.—This paper describes species composition and density changes in rodent populations during postfire succession following prescribed fire in the chaparral community of the San Gabriel Mountains. Conclusions are drawn from a 4-year, live-trap, mark and release study of postfire succession in two watersheds receiving "hot" burns and two receiving "normal" burns.

for climatic conditions at the time. A fifth watershed (803), which has been extensively studied since 1976 (see Wirtz 1977, 1979, 1982, 1984), serves as a control for studies on the prescribed burn areas.

Rodent live-trap, mark and release, studies were conducted on all experimental areas prior to the burns to document the size and species composition of the prefire rodent community on all watersheds, and 175 individuals were permanently marked by toe-clipping to provide a prefire pool of marked rodents from which to determine survival rates following the burn. Following the fire grids of 50 stations at 15 m intervals were established in each of the four watersheds on the sites of the prefire censusing, and a live-trap, mark and release, program was initiated to determine fire survival and postfire rodent succession patterns.

For this paper, population estimates were done by the Hayne (1949) equation. Area sampled, for each species, for each month, was estimated by determining the mean distance traveled for each species between captures, for each month, and then adding a zone equal to the mean distance travelled to the perimeter of the grid. Biomass was determined by the product of the estimated population times the mean weight for each species for the month, and these values are then summed for all species taken on the grid for the month.

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Results

Postfire trapping was initiated in February 1985, and both experimental and control plots were sampled bi-monthly. Hayne equation population estimates for rodent populations on each study plot are presented in figures 1-5. The absence of data points from February through April or May means that no rodents were trapped, except for watershed 803 in which trapping was not begun until June 1985.

Mice of the genus *Peromyscus* (deer mouse, *P. maniculatus*; brush mouse, *P. boylii*; California mouse, *P. californicus*), and California pocket mice, *Perognathus californicus*, constitute the bulk of the postfire rodent population. Pacific kangaroo rat, *Dipodomys agilis*, dusky-footed wood rat, *Neotoma fuscipes*, and California vole, *Microtus californicus*, are present in low numbers, and a few Botta's pocket gopher, *Thomomys bottae*, and

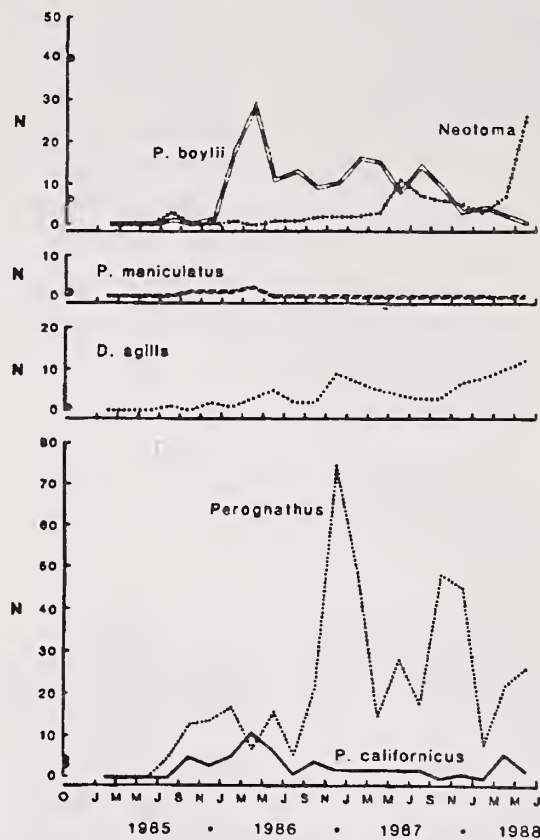


Figure 2.—Hayne equation estimates of population size of rodent species in Bell 804, normal prescribed burn. Note that points at 0 on the x-axis against the y-axis are populations estimates prefire.

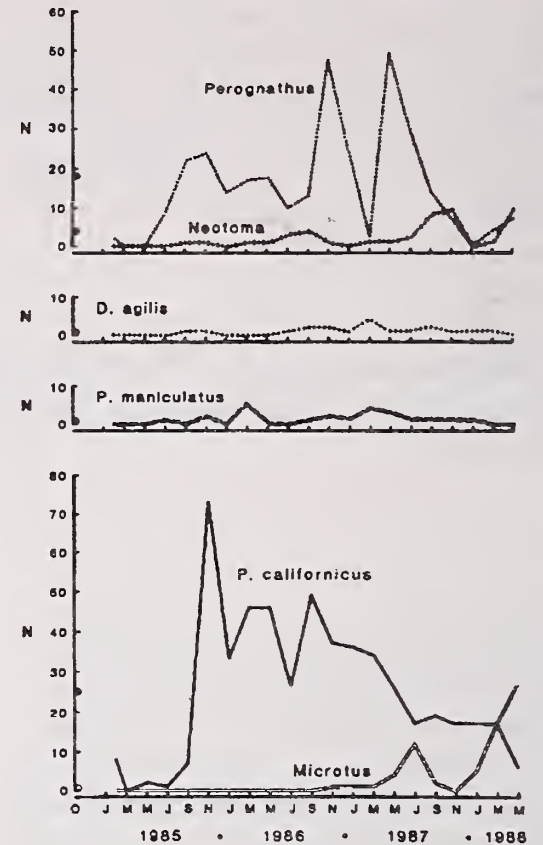


Figure 4.—Hayne equation estimates of population size of rodent species in San Dimas 776, normal prescribed burn. Note that points at 0 on the x-axis against the y-axis are populations estimates prefire.

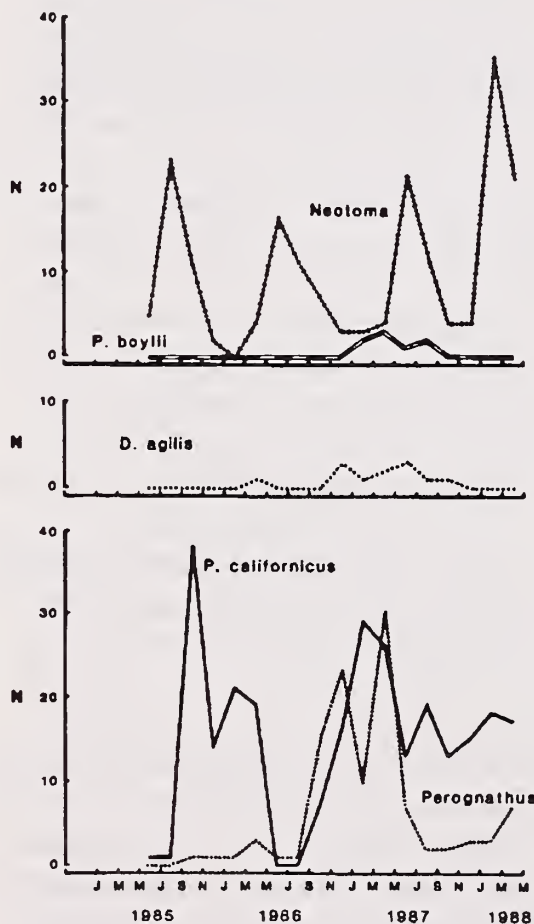


Figure 1.—Hayne equation estimates of population size of rodent species in Bell 803, the 28-year-old chaparral control plot.

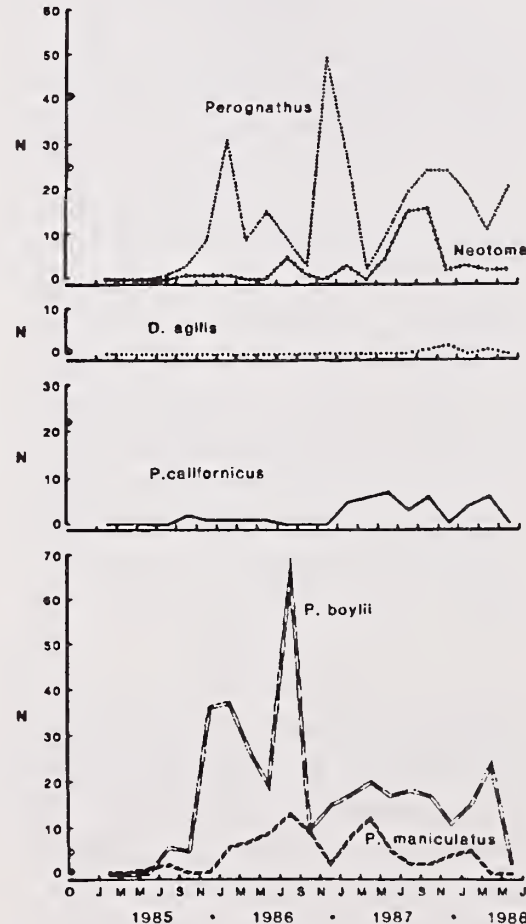


Figure 3.—Hayne equation estimates of populations size of rodent species in Bell 874, hot prescribed burn. Note that points at 0 on the x-axis against the y-axis are populations estimates prefire.

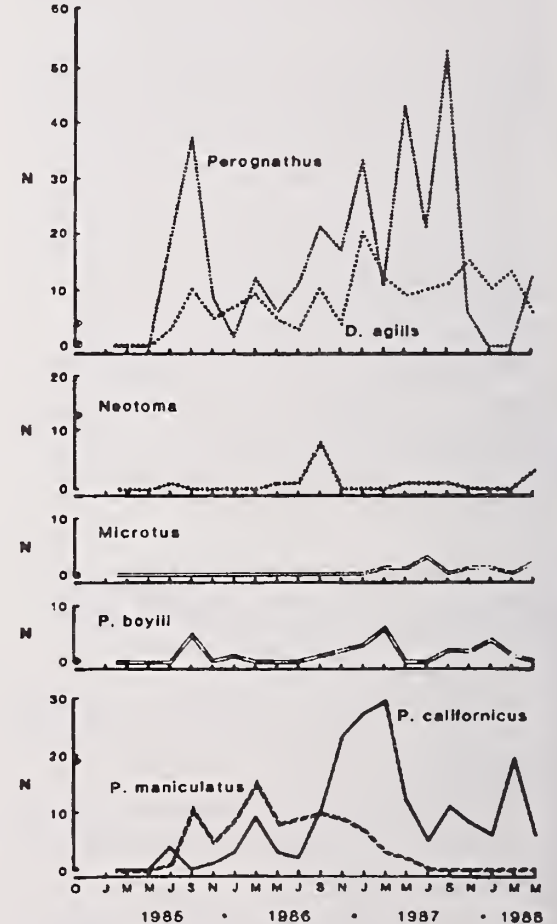


Figure 5.—Hayne equation estimates of population size of rodent species in San Dimas 775, hot prescribed burn. Note that points at 0 on the x-axis against the y-axis are populations estimates prefire.

western harvest mouse, *Reithrodontomys megalotis*, have also been taken. Larger mammals observed in burned watersheds, for which no quantitative data are available, included Beechey ground squirrel, *Spermophilus beecheyi*, Audubon's cottontail, *Sylvilagus auduboni*, brush rabbit, *S. bachmani*, coyote, *Canis latrans*, black bear, *Ursus americanus*, badger, *Taxidea taxus*, and mule deer, *Odocoileus hemionus*.

Fire Survival

No marked wood rats survived the fires. Nine (12.5%) *Peromyscus* survived normal fires, and one (1.4%) survived hot fires. Tow (12.5%) Pocket mice survived normal fires, and two (12.5%) Survived hot fires. These data support the currently held opinion that some rodents do survive fires, and help provide the nucleus, along with immigration from unburned areas, for rodent postfire succession.

Larger mammals seen in the burned watersheds in the first month postfire included coyote, black bear, badger, and mule deer.

Early Postfire Succession

Pocket mice and all three *Peromyscus* species were present on one hot burn (874) by April 1985, six months postfire, but no rodents were present on the other hot burn (775). Pocket mice moved into this hot burn (775) by May, and two *Peromyscus* species, (*P. californicus*, *P. maniculatus*) were present by July.

Pacific kangaroo rats appeared on some burned areas by June or July 1985 (they are rare in mature chaparral). Woodrats appeared on one normal burn (804) by June 1985, and another (776) by September 1985, and on one hot burn (874) by August 1985. Single pocket gophers and harvest mice have been taken on one hot burn (775).

Demography

Sampling was not begun on the control plot (803) until June 1985. The rodent population on this plot consists chiefly of wood rats, California mice, and pocket mice (fig. 1). The California mouse population peaked during the fall, winter, and spring of 1985-86, and again in the winter and spring of 1986-1987. Pocket mice were rare on the control until the fall of 1986 and remained common until the summer of 1987 (fig. 1). The wood rat population has peaked in each summer studied to date.

The prefire rodent population on the normal burn in Bell (804) was composed primarily of woodrats, with smaller numbers of other species (fig. 2) (note that symbols at 0 on the x-axis against the y-axis represent prefire density estimates). The postfire rodent population on this grid has been composed primarily of brush mice and pocket mice, with population peaks of the latter in each winter (1985, 1986, and 1987). Wood rat populations did not show significant increases on this grid until the spring of 1987, about 30 months after the burn, and they have yet (June 1988) to reach prefire densities (fig. 2). Pacific kangaroo rats have occurred on this burned area in numbers above prefire densities since the summer of 1985. Brush and California mouse populations have occurred in numbers above prefire densities since the winter of 1985-86 (fig. 2).

The prefire rodent population on the hot burn in Bell (874) was composed largely of wood rats, California mice, and pocket mice (fig. 3). All species, except kangaroo rats, were present again on this grid by August 1985, 10 months postfire. The postfire rodent community on this hot burn has been dominated by brush mice and pocket mice (fig. 3), with both species reaching, or exceeding, prefire densities by the winter of 1985, approximately a year after the burn. California mouse and wood rat

populations have yet (June 1988) to reach prefire densities (fig. 3).

The prefire rodent population on the normal burn in San Dimas (776) was composed primarily of California mice and wood rats, with smaller numbers of pocket mice and no brush mice (fig. 4). The postfire rodent community has been dominated by California mice and pocket mice, with both species exceeding prefire densities by the winter of 1985, approximately one year postfire. Wood rats have yet (June 1988) to reach prefire densities, brush mice have not appeared on this grid, and California voles were common in the summer of 1987 and the spring of 1988 (fig. 4).

The prefire rodent population on the hot burn in San Dimas (775) was very similar to that on the normal burn here (fig. 5). And, like the normal burn, the postfire community has been dominated by California mice and pocket mice, with pocket mice exceeding prefire densities by the summer of 1985 and California mice exceeding prefire densities by the fall of 1986 (fig. 5). Pacific kangaroo rats also exceeded prefire densities within one year postfire on this grid.

Comment should be made about the presence of deer mice (*P. maniculatus*) and California voles (*Microtus*) on these grids. Neither species was present on any grid prefire, and neither has been taken on the control (figs. 1-5). *P. maniculatus* has been taken on all burned grids, with peaks of abundance by the second year postfire and declining abundance by the fourth year postfire (figs. 4 and 5).

Effects of Hot and Normal Fires

The effects of hot and normal fires on rodent demography were examined by (1) comparing pre and post fire populations in areas exposed to these two fire regimes (figs. 6 and 7), (2) comparing the number of captures of each species postfire under each fire

regime (fig. 8), and (3) comparing total postfire biomass on areas exposed to different fire regimes (fig. 9) (note again that points at 0 on the x-axis against the y-axis are prefire populations estimates). Only species with relatively high abundances are considered in this paper.

Prefire populations of brush mice were essentially the same on both areas to be burned in Bell, while densities of pocket mice and California mice were greater on the area to receive the hot burn, and deer mice were not present on either grid (fig. 6). All prefire populations were severely impacted by fire, dropping in most instances to near zero for several months postfire. Pocket mice increased to twice their prefire density on the hot burn and 25 times prefire density on the normal burn (fig. 6). Brush mice increased to 14 times their prefire density on the hot burn and six times prefire density on the normal burn (fig. 6). California mice returned to prefire density by one year postfire on the normal burn, and numbers have remained relatively constant since then. Deer mice were present on both burned areas postfire, but have been more abundant on the hot burn (fig. 6).

Prefire populations of California mice and pocket mice were similar on both areas to be burned in San Dimas (fig. 7). Some individuals survived the normal burn. Pocket mouse populations exceeded prefire densities on both normal and hot burns by eight months postfire (fig. 7). California mouse populations exceeded prefire densities by one year postfire on the normal burn, but took two years to reach prefire densities on the hot burn (fig. 7). Two species not present prefire, Pacific kangaroo rats and deer mice, colonized both burned areas by eight months postfire; kangaroo rats have remained numerous on the hot burn, and deer mice are more numerous on the hot burn than on the normal burn (fig. 9).

Captures of California mice postfire are greater on normal burns

than on hot burns, and exceed captures on the control on one normal burn (776) (fig. 8). Captures of brush mice postfire are greater on both hot burns and one normal burn than on the control, and captures on hot burns are greater than on normal burns for each pair of watersheds burned (fig. 8). Deer mice have not been captured on the control; captures are greater postfire on hot burns than on normal burns for each pair of watersheds burned (fig. 8). Captures of wood rats are less on all burned areas than on the control, and they are less on hot burns than on normal burns for each pair of watersheds burned (fig. 8).

California voles have not been taken postfire on the control nor on one normal burn, and are greater on the other normal burn than on either hot burn (fig. 8). Captures of Pacific kangaroo rats postfire are greater on

both normal and one hot burn than on the control, while captures of pocket mice postfire are greater on all burned areas than on the control (fig. 8).

Total biomass on the control, not 28 years old, has fluctuated during the period of study, but shows a slight increasing trend (fig. 9). Total biomass on both burned plots in Bell, the location of the control, has also fluctuated, with a slight increasing trend, in a fashion similar to that of the control (fig. 9). Total biomass on the burned plots in San Dimas has also fluctuated, with slight increasing trend, but with two dramatic biomass increases, one in the Spring of 1987 and the other in the spring of 1988 (fig. 9). The pattern of fluctuation, and increase, on the normal burn in San Dimas is similar to that observed for the control, and the pattern of fluctuation, and increase, if

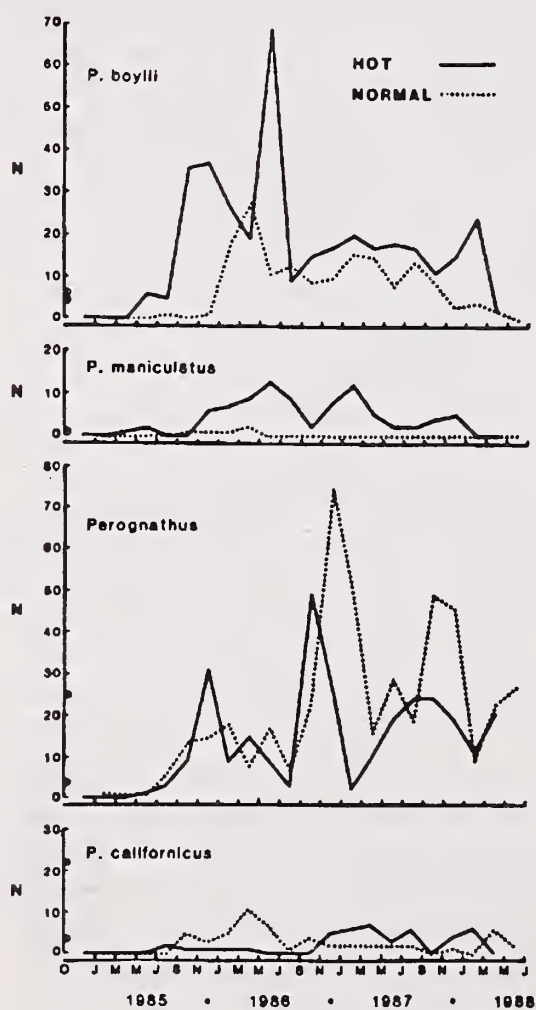


Figure 6.—Comparison of rodent postfire population growth on normal (804) and hot (874) prescribed fire plots in Bell. Note that points at 0 on the x-axis against the y-axis are populations estimates prefire.

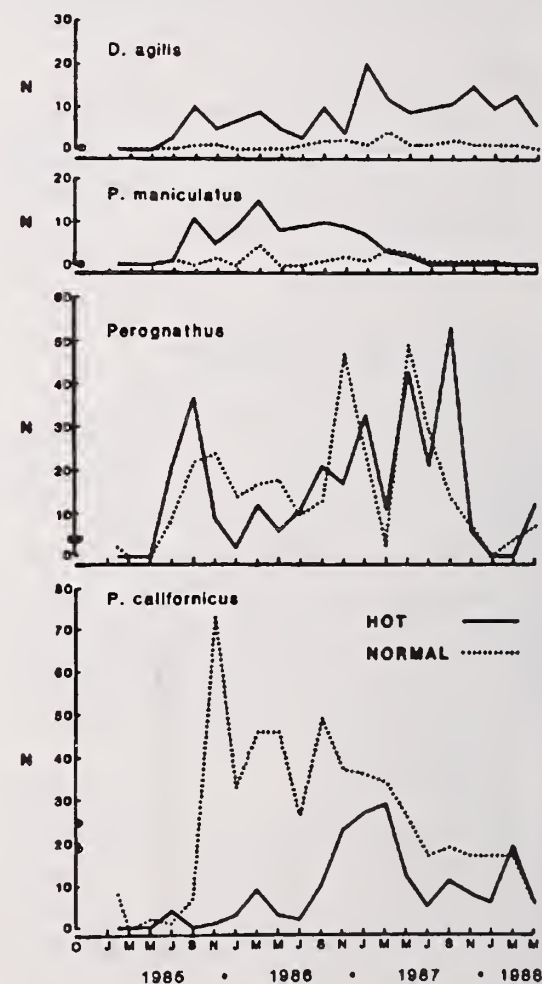


Figure 7.—Comparison of rodent postfire population growth on normal (776) and hot (775) prescribed fire plots in San Dimas. Note that points at 0 on the x-axis against

the two sharp peaks are not considered, is also similar to the control (fig. 9).

Discussion

General patterns of rodent postfire succession following these prescribed burns are similar to those reported by Wirtz (1977, 1982, 1984) for succession following wildfire in the chaparral of the San Gabriel Mountains, but lack the dramatic increases in density, and therefore biomass, observed in these earlier studies. He notes (1984) that rodent succession following wildfire takes about four years before populations stabilize at essentially prefire conditions found in older chaparral stands. The response of species to these prescribed fires varied, with some species reaching prefire densities in less than four years and others having not yet reached prefire densities at essentially four years postfire.

Only slight differences are noted between rodent postfire succession

on normal and hot burns, and these may probably be attributed to differences in the biology of individual species. In Bell, both normal and hot burns were dominated postfire by pocket mice and brush mice, though pocket mice had the highest density on the normal burn (804) and brush mice had the highest density on the hot burn (874) (fig. 6). California mice recovered to prefire density on the normal burn, but have not yet (June 1988) recovered on the hot burn, and wood rats have not recovered to prefire densities on either burned area (fig. 6). Deer mice have been more prevalent on the hot burn than on the normal burn during the period of the study. By the second year postfire, populations of all species, except wood rats, exceeded prefire densities on the normal burn (fig. 2), and populations of brush mice and pocket mice had exceeded prefire densities on the hot burn (fig. 3).

In San Dimas, where considerable brush was left alive on the normal burn (776), both normal and hot burns were dominated postfire by

pocket mice and California mice (fig. 7). Both of these species recovered to prefire densities on the normal burn by one year postfire (fig. 4), as did pocket mice on the hot burn (fig. 5), but California mice did not reach prefire densities on the hot burn until the second year postfire (fig. 5). For reasons not immediately apparent, but probably because of the presence of some grass prefire, California voles were found only in these two watersheds postfire. The greater relative abundance of Pacific kangaroo rats on the hot burn is most likely due to the fact that more open space, necessary for kangaroo rat saltatorial locomotion, was left by the hot fire here.

Pocket mice increase rapidly on burned areas, there being essentially no difference between normal and hot burns (figs. 6 and 7). Brush mice, if present prefire, recover more rapidly postfire than California mice, and the latter recover more rapidly on normal burns than on hot burns (figs. 6 and 7). Deer mice, virtually nonexistent in mature chaparral, colonize both normal and hot burns, and increase more rapidly on hot burns (figs. 6 and 7).

Data on captures (fig. 8) indicate that increase of deer mice on hot burns. The species is known to colonize disturbed areas, whether they be caused by fire, logging, or over-

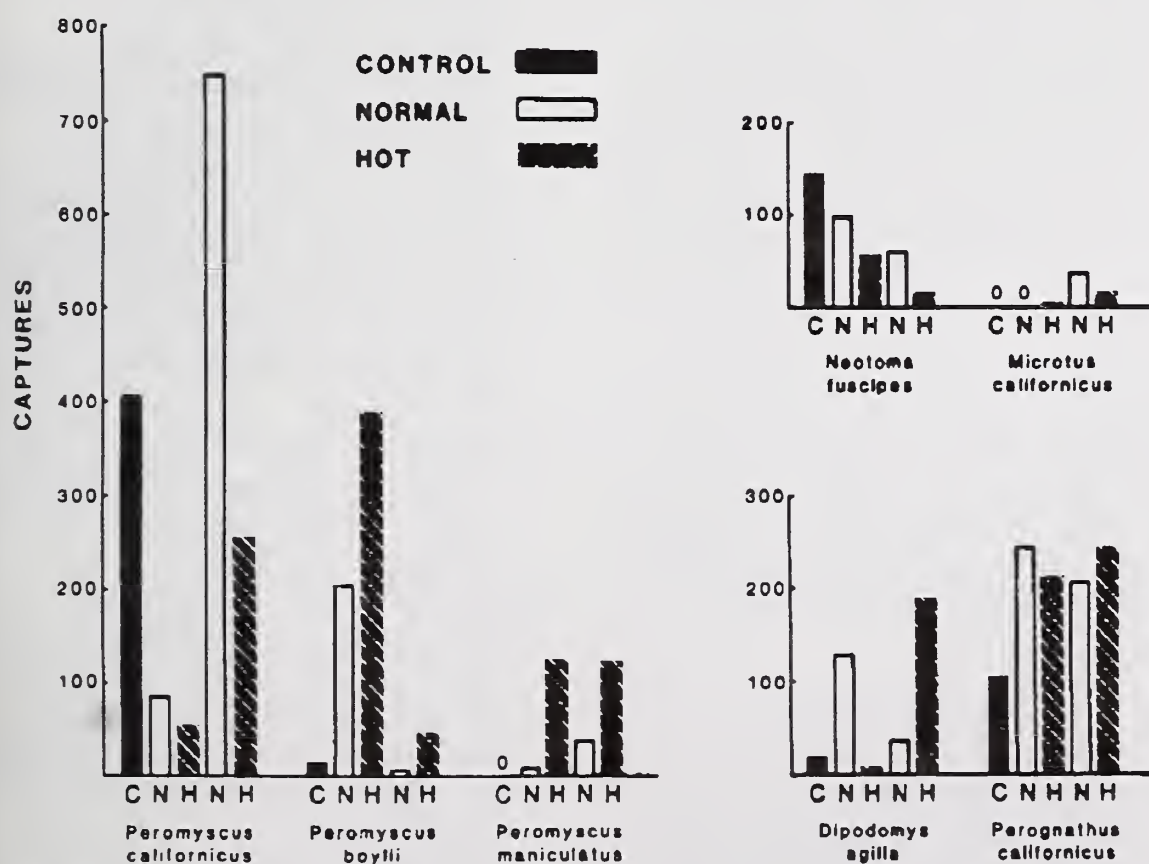


Figure 8.—Comparison of postfire captures of all rodent species on control and prescribed burn plots.

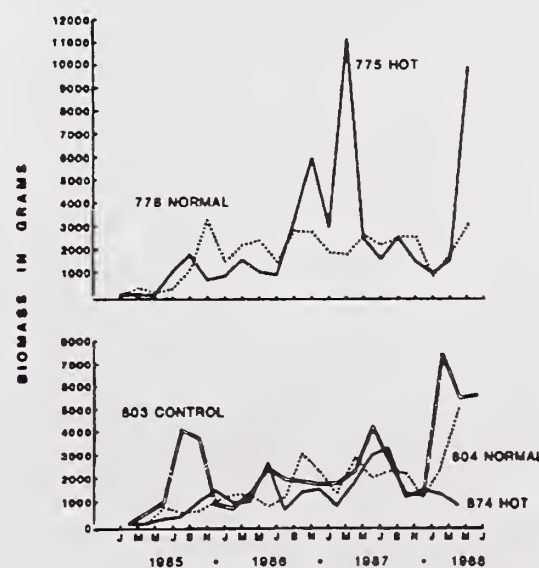


Figure 9.—Total postfire biomass (grams) for control and burned plots.

grazing (Williams 1955). These data also illustrate the decline of California mice on hot burns and its increase in normal burns, and the increase of brush mice, where present prefire, on both normal and hot burns. Burning favors density increases of pocket mice, with essentially no difference between normal and hot burns. Kangaroo rats exhibit variable increases in response to fire, and wood rats are severely impacted by fire.

Biomass increases in response to fire are variable, and in this study, were similar in variability to those occurring on the control (fig. 9). The sharp peaks in biomass observed on one hot burn (775) are due to large density increases in pocket mice during these periods.

It is important to note, when comparing data for normal and hot burns, that in one normal burn (776) a lot of unburned brush remained, perhaps more accurately simulating an "island" in a burn rather than a burn per se. So, for this study, the data for 776 are somewhat atypical, and 804 represents more accurately the situation following a normal burn. But it is also important to note that "islands" of unburned vegetation are frequently left by wildfire, providing refugia for both plants and animals from fire.

Several general conclusions may be drawn from the rodent data: (1) fire may impact rodent species severely, probably chiefly through loss of habitat resources, especially shelter and food; (2) some individuals survive fire; (3) colonization from adjacent habitats may be rapid; (4) postfire succession is somewhat dependent on prefire species composition of the area; (5) in southern California chaparral, at least two species, deer mouse and California vole, are fire specialists, entering the system only for relatively short periods of the postfire succession; (6) species requiring brush for cover and/or food, like wood rats and California mice, are most severely impacted by

fire, and require the longest time to recover to prefire densities; (7) there is no clear-cut difference in rodent postfire succession following normal and hot fires; (8) rodent postfire succession is characterized by increases in successional-adapted species, with declines in those species for which essential habitat features are lacking; and (9) recovery of the rodent community to its prefire condition probably takes four to six years, with the exact pattern of recovery being dependent on prefire species composition and features of the prefire plant community and postfire plant succession that have not been delineated.

Acknowledgments

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Douglas-Fir Forests in the Cascade Mountains of Oregon and Washington: Is the Abundance of Small Mammals Related to Stand Age and Moisture?¹

Paul Stephen Corn,² R. Bruce Bury,³ and Thomas A. Spies⁴

Management of old-growth Douglas-fir (*Pseudotsuga menziesii*) forests west of the Cascade Mountains in the Pacific Northwest is an increasingly controversial topic, arising from a fundamental conflict. These forests are extremely valuable sources of timber; 40 ha of old growth is valued at about \$1.6 million (Meslow et al. 1981). At the same time, conservationists view old growth as a unique ecosystem that is nonrenewable under current management practices (Cutler 1984, Schoen et al. 1981). Old-growth forests are disappearing; during the past 30 years, removal of Douglas-fir saw timber from western Oregon and Washington has exceeded annual growth by a factor of three (Harris 1984). Now, less than 20% of the original old-growth forest in the Pacific Northwest remains (Spies and Franklin in press).

Historically, old-growth forests were viewed as decadent stands of

wasted timber that provided little wildlife habitat. For example, Tevis (1956) stated:

Virgin forest in the Douglas-fir (*Pseudotsuga taxifolia* [*menziesii*]) region of northwestern California is sterile habitat for wildlife. Dense shade and competition from large old trees prevent the growth of nearly all bushy and herbaceous vegetation except a weak understory of tan oak (*Lithocarpus densiflora*). Food for animals is scarce.

The value of old growth has been rehabilitated. Currently, old-growth Douglas-fir forests are considered excellent wildlife habitats, dominated by large trees, but possessing a complex and varied structure (Franklin et al. 1981, Franklin and Spies 1984), including some of the highest amounts of coarse woody debris (CWD) reported for any forest ecosystem (Spies et al. in press).

Most remaining old growth in the Pacific Northwest is on Federal land managed by the Forest Service and Bureau of Land Management (Harris 1984). The policy of the U.S. Department of Agriculture is to "...maintain viable populations of all existing native vertebrate populations..." (Cutler 1980) but, until recently, the information needed to achieve this goal did not exist. Most lists of species with some degree of dependence on

Abstract.—Red tree voles (*Arborimus longicaudus*) were the only small mammal strongly associated with old-growth forests, whereas vagrant shrews (*Sorex vagrans*) were most abundant in young forests. Pacific marsh shrews (*S. bendirii*) were most abundant in wet old-growth forests, but abundance of this species in young (wet) forests needs further study. Clearcuts had a mammalian fauna distinct from young forest stands. Abundance of several species was correlated to habitat features unique to naturally regenerated forests, indicating an urgent need to study the long-term effects of forest management on nongame wildlife.

or association with old growth are incomplete or inferential (e.g., Harris and Maser 1984, Meslow et al. 1981). Recent research has improved this situation, but little of it is directed toward nongame species. A recent symposium on wildlife and old-growth relations (Meehan et al. 1984) included 27 papers. Two-thirds (17) of the papers concerned game species, and only four papers discussed ecology of nongame wildlife. Remaining papers discussed either characteristics of old-growth forests (three papers) or management objectives (three papers).

In 1981, to provide the information necessary for managing wildlife in the national forests of the Pacific Northwest, the U.S. Forest Service chartered the Old-Growth Wildlife Habitat Program⁵ (OGWHP). Its goals (Ruggiero and Carey 1984) were to: (1) identify old-growth forests were unique components of coniferous forest ecosystems, (2) identify the ecological characteristics of old growth, (3) identify any wildlife species dependent on old growth for survival or optimal habitat, and (4) determine the amount and distribution of old growth necessary to meet the needs of dependent species.

Vegetation and vertebrate community studies were performed on a matrix of forest conditions in naturally regenerated stands. Forest de-

⁵Now the Wildlife Habitat Relationships in Western Oregon and Washington Project.

¹Paper presented at symposium, Management of Amphibians, Reptiles, and Small Mammals in North America. (Flagstaff, AZ, July 19-21, 1988.)

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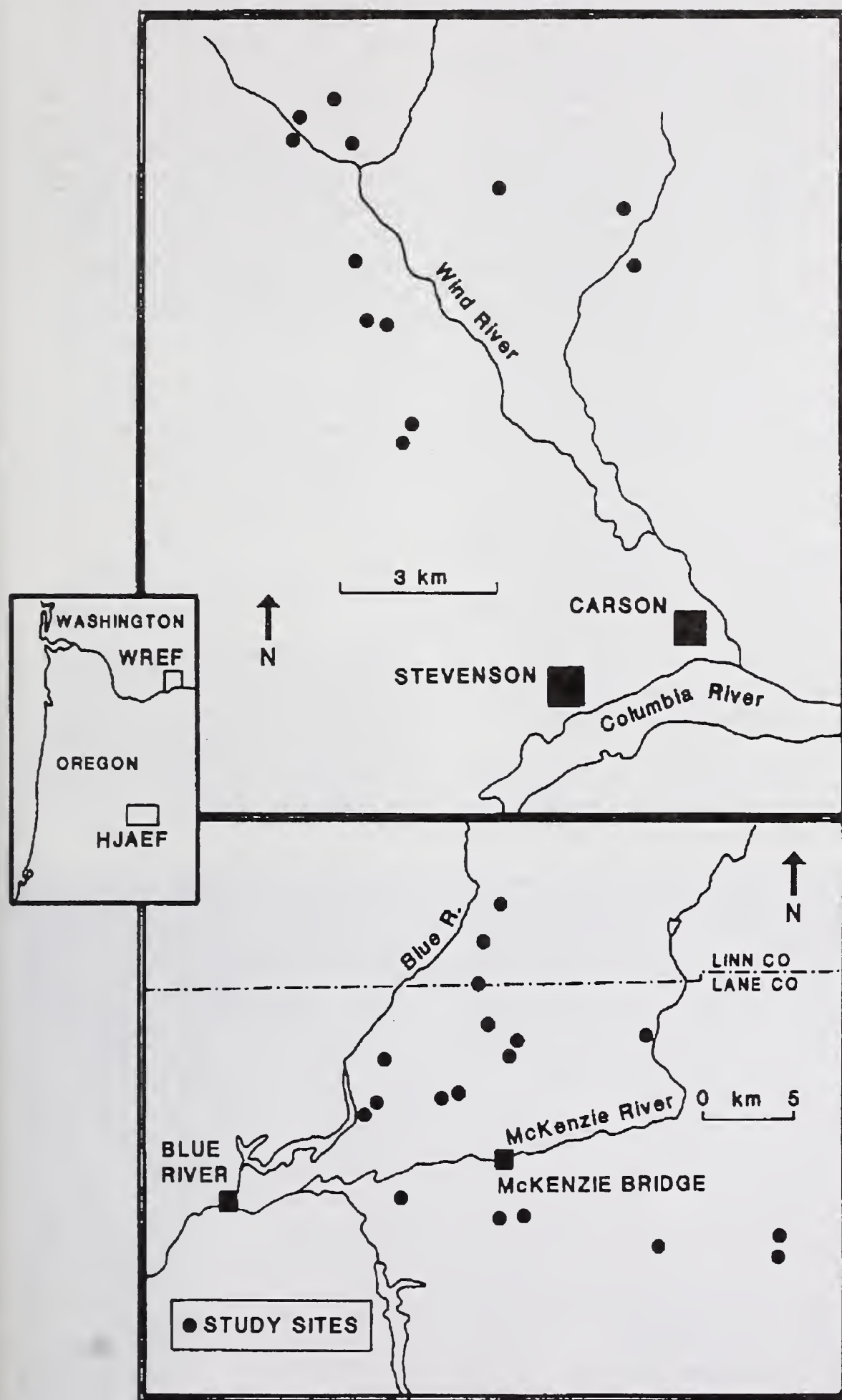


Figure 1.—Maps of study areas where pitfall trapping was conducted in 1983. HJAEF = H. J. Andrews Experimental Forest; WREF = Wind River Experimental Forest. Note that the scale for each map is different.

velopment was examined across a chronosequence, and a moisture gradient was examined for the old-growth stands.

Field work began in 1983 with vegetation and vertebrate community pilot studies at 30 stands spread between two sites in the Oregon and Washington Cascade Mountains. The primary goal of the first year was to evaluate and recommend sampling techniques. The pilot studies were successful in developing and refining sampling methods (e.g., Bury and Corn 1987, Thomas and West 1984, West 1985). In 1984 and 1985, community studies expanded to more than 180 stands in the Washington Cascades, the Oregon Cascades, the Oregon Coast Range, and the Siskiyou and Klamath mountains of southern Oregon and northern California. Since 1985, species-specific studies have been emphasized, largely concerning the ecology and management of the spotted owl (*Strix occidentalis*) and its prey base.

Our paper concerns the community ecology of small mammals as revealed by pitfall trapping in 1983. The data collected in 1983 are useful for other than evaluating techniques, but these data are difficult to integrate into 1984 and 1985 results, because the sampling methods were changed (Bury and Corn 1987). Therefore, we report these results with the caveat that variation between years is not examined.

Our specific objectives are to examine the relations of the abundance of small mammal species to the chronosequence and the moisture gradient and to identify specific habitat features that contribute to abundance. The effects of forest management are also discussed.

METHODS

Study Areas

Forest stands were studied in two areas on the western slopes of the

Cascade Mountains (fig. 1). Twelve stands were in the Wind River Experimental Forest (WREF) or the surrounding Gifford Pinchot National Forest, Skamania County, Washington, and 18 stands were in the H. J. Andrews Experimental Forest (HJAEF) or Willamette National Forest, Lane and Linn counties, Oregon. Appendix A lists ages, elevations, and locations of all stands.

Stand Selection and Classification

Initial stand selections were made by OGWHP investigators studying the structure of old growth (Franklin and Spies 1984, Spies and Franklin in press). Age was the primary criterion for establishing a stand's position on the chronosequence. Topographic position and understory vegetation provided a first approximation of a moisture gradient (south- or west-facing ridges were generally dry, whereas stands on north-facing slopes were usually moist to wet). Most stand boundaries were not highly distinct (e.g., forest islands surrounded by clear cuts) but were determined by several factors, including age, disturbance history, vegetational composition, physiography, and soils. Stands were first chosen from aerial photographs and forest type maps, but an on-site inspection was completed before any of the vertebrate sampling plots were established. Stand sizes varied from about 10 to 20 ha.

Coarse woody debris (CWD), vegetation, and site characteristics were sampled in five nested, circular plots in each stand (Spies et al. in press). Classification of downed CWD (=logs) followed Franklin et al. (1981) and Maser and Trappe (1984): from class 1 logs (essentially undecayed) to class 5 logs (well decayed, appearing as raised hummocks in the forest floor).

The chronosequence consisted of four categories beginning with clearcuts (< 10 years old), closed-can-

opy young stands (30-80 years), mature stands (80-195 years), and old growth (195-450 years). The latter three categories were all composed of naturally regenerated forests. Ages of young and mature stands were estimated by increment coring of at least five dominant Douglas-fir trees per stand (Spies et al. in press). Ages of old-growth stands were estimated from increment cores and by examining stumps in adjacent clearcuts and roadsides.

In an ideal chronosequence analysis, age classes should have similar means and ranges of site characteristics. We were only partly successful in achieving this goal, because the age classes were not equally distributed over the landscape, and other criteria such as stand size, accessibility, and absence of logging activity took precedence over site uniformity. Consequently, young and mature stands spanned a wider range of environments than originally planned and for some variables (such as elevation at the HJAEF), the younger age classes differed from old growth.

We conducted analysis of moisture effects across the old-growth

stands. Adjustments were made to the preliminary field classification of dry (OGD), moderate (OGM), and

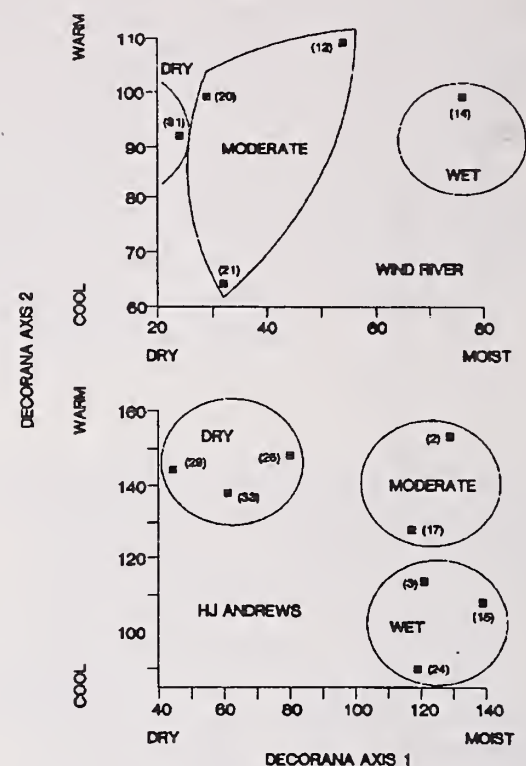


Figure 2.—Detrended correspondence analysis (DECORANA) of percent occurrence of understory plant species in old-growth stands in Oregon and Washington. Stands were placed in moisture categories (wet, moderate, or dry) based on their relative positions on the two gradients.



Figure 3.—A pitfall array in clearcut stand #291 in Oregon. Photo by L. Hanebury.

wet (OGW), after conducting ordinations of old-growth stands using detrended correspondence analysis (DECORANA). DECORANA is a weighted average technique that is computationally related to principal components analysis (Gauch 1982). The percent occurrence of understory plant species in five 1,000-m² plots in each stand was used in separate analyses of each study area (fig. 2). The first axis in both areas separated stands along a moisture gradient correlated with indicators of topographic moisture, such as aspect and slope. The second axis in both analyses separated stands along a complex gradient of temperature and moisture and was correlated with elevation.

Pitfall Trapping

We installed a pitfall trap array (fig. 3) in each stand. An array included two triads, 25 m apart, each consisting of three 5-m long aluminum drift fences with screen wire funnel traps on each side and pitfall traps at each end. Thus, each array had six fences and twelve pitfall and twelve funnel traps. Bury and Corn (1987, this volume) provide more complete descriptions and illustrations.

The traps were opened the last week in May 1983 and were operated continuously for 180 days. No water was put in traps, because this has a deleterious effect on the preservation of amphibians, which were a major target of the traps (Bury and Corn, this volume). In practice, most traps accumulated some water and most mammals drowned. Traps were checked initially every three days, but as trap rate declined over time, the interval between checks increased to about seven days.

Mammals taken from traps were identified, sexed, measured, and preserved as skulls, skeletons, or skins and skulls. All specimens from Oregon and most from Washington were deposited in the National Museum of

Natural History (USNM), where all identifications were verified. Common and scientific names used in this paper follow Banks et al. (1987).

We encountered one problem that significantly affected the data analysis. The high trap success at the WREF stands exceeded the field crew's ability to process specimens, and approximately 25% of the mammals were discarded in the field. When the remaining specimens were examined later at the USNM, about 10% of the field identifications of Trowbridge's shrews (*Sorex trowbridgii*), montane shrews (*S. monticolus*), and vagrant shrews (*S. vagrans*) were inaccurate. Thus, the exact numbers of these shrews captured at WR are in doubt (Bury and Corn 1987), and analyses of overall species richness and individual abundance of these species were only reported for Oregon data.

Statistical Analyses

We analyzed the mean abundance (total number of captures) of each species, mean total abundance, and mean species richness across each gradient with one-way analysis of variance (ANOVA). No traps were missing or damaged during the 180-day trapping period, so it was unnecessary to adjust raw abundance for trap nights. Scavengers may remove animals from traps when there are long intervals between checks (M. G. Raphael, personal communication), and traps with water may be more effective than dry pitfalls at capturing rodents with good leaping ability. Because 70% of all mammals were captured in the first 60 days of trapping (Bury and Corn 1987), when traps were checked frequently, we feel these considerations are minor and we made no adjustments to the data.

Abundances were log transformed before the ANOVAs were run. Clearcuts, OGW and OGD stands were not included in the ANOVA of

the chronosequence. Clearcuts, young, and mature stands were not included in the ANOVA on moisture (Spies et al. in press). A comparison of species' abundances in clearcuts versus young stands is presented separately. Pearson correlation coefficients were calculated between abundance (transformed as $\ln[\text{abundance} + 1]$) and 24 of the habitat variables (appendix B). Percentage variables (e.g., % cover of grasses) were arcsin transformed, other variables were log transformed. We also performed a principal components analysis using the habitat variables, but because the first three factors explained only 52% of the variation among stands, we report only the significant ($P < 0.05$) bivariate correlations between abundance and individual habitat variables. All analyses were performed using the statistical program SYSTAT⁶ (Wilkinson 1988).

RESULTS

The pitfall arrays were highly effective at capturing small mammals, producing 3,877 captures of 27 species. Insectivores and microtine rodents were best caught by pitfalls, while deer mice (*Peromyscus maniculatus*) were under-sampled (Bury and Corn 1987). Captures of each species in each stand are listed in tables 1 (HJAEF) and 2 (WREF).

Mean species richness (number of species) varied from about nine in mature stands to 12 in OGW stands (fig. 4). There was no significant difference across either the chronosequence or the moisture gradient. Total abundance was highest in young and mature stands and lowest in OGM stands, but the difference was not significant. There was no apparent trend in small mammal abundance across the moisture gradient.

⁶Trade names are provided for the benefit of the reader; such use does not constitute an official endorsement by the Fish and Wildlife Service.

Table 1.—Abundance of small mammals captured at the H. J. Andrews Experimental Forest in Oregon. Arrays of pit-fall traps with drift fences were operated continuously for 180 days in 1983.

Species	Stand no.	Old growth									Mature			Young				Clearcut		
		Wet			Moderate			Dry			11	35	42	39	47	48	75	55	291	391
Trowbridge's Shrew		33	48	48	76	35	60	75	70	51	56	78	70	139	71	83	18	39	17	
Montane Shrew		16	15	28	23	13	9	7	19	15	16	15	26	17	14	22	3	8	13	
Vagrant Shrew		13	2	1			2		4	2	7	2	17	3	5	6	1	1	74	
Pacific Marsh Shrew		7	14	8		1	1	1	1	7	9		2	2	4	13			1	
Northern Water Shrew													4							
Pacific Shrew									1								2			
Unidentified shrews			1		1												1			
Shrew Mole		3	5	3		1	1		2	4	2		9	4	2	5				1
Coast Mole		1		1	4	5	4	6	1	2	2	1		7	1	2	3	2		
Western																				
Red-backed Vole		14	4	1	2	9	6	3	10	6	15	18	52	13	7	4				1
Creeping Vole			1		1	2	1		1	1			2			3	1	5	28	
Red Tree Vole		1	3	3	4	1				1	2				1			1		
Water Vole					1	2	1						1			1				
Heather Vole									1											5
Townsend's Vole			1									2							1	
Deer Mouse		3		3	3	1	3	2	1	3	3		3	1	2	5	2	3	24	
Pacific Jumping Mouse			1	1			2				1		3	1		14		1	3	
Western Pocket Gopher											1	2	1							16
Others ^a			1	2		1		2	2				2		1	1		1	1	

^aTownsend's Chipmunk (8), Northern Flying Squirrel (3), Ermine (2), Spotted Skunk (1), Snowshoe Hare (1).

Table 2.—Abundance of small mammals captured at the Wind River Experimental Forest in Washington. Arrays of pit-fall traps with drift fences were operated continuously for 180 days in 1983.

Species	Stand No.	Old growth					Mature			Young		Clearcut	
		Wet	Moderate			Dry	41	42	50	60	61	70	71
Pacific Marsh Shrew		10	3	2	3		6	3	3	2	7	3	
Other shrews ^a		86	73	93	46	115	192	127	158	117	97	50	86
Shrew Mole		6		9	1	2	9	2	6	1	1		3
Coast Mole			3	3		3	4	1	1	2			
Southern													
Red-backed Vole		15	10	21	20	40	13	16	3	41	31	4	1
Creeping Vole		2		4	2	3	6	9	2	1	4	9	11
Townsend's Vole		1				5	2	1	1	1			5
Other Microtines ^b										3	1		2
Deer Mouse		8	16	40	11	28	23	11	16	9	7	32	7
Pacific Jumping Mouse		2		2			2			1		1	
Northern Pocket Gopher							2		1		1		4
Others ^c			1	1		7					1	1	3

^aunidentified (70), Trowbridge's Shrew (696?), Montane Shrew (351?), Vagrant Shrew (120?), Masked Shrew (?), and Northern Water Shrew (3).

^bunidentified (6), Heather Vole (1).

^cErmine (6), Townsend's Chipmunk (3), Yellow-pine Chipmunk (2), Snowshoe Hare (2), Northern Flying Squirrel (1), Pika (1).

Species-Habitat Associations

Trowbridge's Shrew

These shrews were the most abundant small mammal (about 46% of all captures). At HJAEF, this species was most abundant in young stands (fig. 5), but the variation across the chronosequence was not statistically significant. Most of the high mean abundance in young stands was due to one stand (#47) at HJAEF (table 1). Abundance on the moisture gradient increased from OGW to OGD, but the differences were not significant.

Habitat variables that were positively correlated with abundance of Trowbridge's shrews included the total basal area and mean diameter at breast height (d.b.h.) of live trees, the number of decay class 4 and 5 (most decayed) downed logs, and litter depth (table 3). Variables negatively

correlated were percent cover by herbs and grasses and the biomass of least decayed logs (class 1 and 2).

Montane Shrew

This was the second most abundant species, occurring in similar numbers in stands of different ages (fig. 5). There is a trend on the moisture gradient of decreasing abundance from OGW to OGD, but the differences are not significant. Abundance of montane shrews was positively correlated with tree size (MDBH) and negatively correlated with percent cover by grasses and number of decay class 1 and 2 logs (table 3).

Vagrant Shrew

Vagrant shrews were significantly less abundant in older forest stands (fig. 5, $P = 0.02$), and variation across the moisture gradient was not significant. This species reached its greatest abundance in one clearcut (see below). Abundance of vagrant shrews was negatively correlated with several characters associated with old-growth forests: number of decay class 4 and 5 logs, percent cover by mosses, litter depth, and slope (table 3).

Pacific Marsh Shrew

The Pacific marsh shrew (*Sorex bendirii*) is a large shrew generally associated with small streams and swamps (Maser et al. 1981, Whitaker and Maser 1976). Our results agree. The greatest abundance was in OGW stands (fig. 5), and the difference across the moisture gradient was significant ($P < 0.001$). Marsh shrews were captured (albeit in low numbers) in moderate and dry old-growth stands where the pitfall arrays were some distance from flowing or standing water, but many of the younger stands in which this species occurred (e.g., stands 11, 35, and 75 at the HJAEF) contained streams

or ponds. Variation across the chronosequence was not significant, but this may be misleading given the high abundance in OGW stands. Our study design precluded us from determining whether Pacific marsh shrews would be abundant in younger wet stands.

Several habitat variables were associated with abundance of Pacific marsh shrews. Positive correlations reflected older, wet forests and included litter depth, total density of live trees, mean d.b.h., and biomass of class 4 and 5 logs. The number of decay class 1 and 2 logs and slope were negatively correlated with abundance (table 3).

Shrew Mole

Shrew moles (*Neurotrichus gibbsii*) are small moles but are more like shrews in appearance and habits. Patterns of their abundance were similar to the Pacific marsh shrew (fig. 5). Shrew moles were most abundant in OGW, but there were no significant differences across the moisture gradient or the age gradient. Unlike the marsh shrew, none of the habitat variables were correlated with abundance.

Coast Mole

We captured 59 coast moles (*Scapanus orarius*), a form rarely taken by conventional snap- or live-trapping techniques. This species might be more active on the surface than other moles (Maser et al. 1981), or our drift fences (which were sunk 20-30 cm into the ground) might have interrupted their burrowing (Williams and Braun 1983). There was no significant variation on the chronosequence, but there was on the moisture gradient ($P = 0.05$). Coast moles were most abundant in OGM and OGD stands and were virtually absent from OGW stands (fig. 5).

Coast moles might prefer well-drained soils (Maser et al. 1981). This

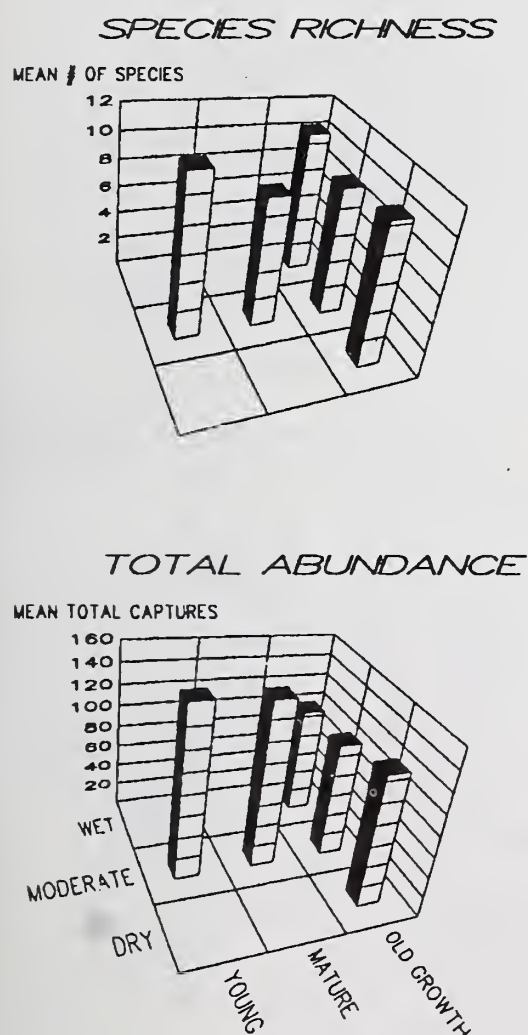


Figure 4.—Mean species richness (HJAEF only) and total abundance (all stands) of small mammals in closed-canopy stands.

is supported by their low abundance in OGW stands where soils are saturated for long periods. Abundance of coast moles was positively correlated with percent cover by deciduous trees. Habitat variables negatively correlated were the number of decay class 3 logs and the number of large-diameter logs.

Red-Backed Voles

We captured two species of red-backed voles: the southern red-backed vole (*Clethrionomys gapperi*) at WREF, and the western red-backed vole (*C. californicus*) at HJAEEF. We caught more southern than western red-backed voles (fig. 6), but the patterns of abundance were similar. Both species were combined in the ANOVAs to maximize the sample size. No differences were detected on either the age or moisture gradients.

Habitat variables were tested separately for each species, but the results were similar (table 4). Abundance of western red-backed voles was positively correlated with total basal area of live trees, mean d.b.h., and percent cover by evergreen shrubs (mainly Oregon grape, *Berberis* spp., and salal, *Gaultheria shallon*).

Negative correlations were with grass cover, biomass of decay class 1 and 2 logs, and aspect (abundance was greatest on southern exposures). Southern red-backed voles were positively correlated with density and basal area of live trees, and mean d.b.h., and were negatively correlated with grass cover.

Red Tree Vole

This species has been identified as an old growth associate (Meslow et al. 1981) and is a major food item of the spotted owl (Forsman et al. 1984). We captured only 17 red tree voles (*Arborimus longicaudus*) in the standard arrays, too few to run the

ANOVA. But, 12 voles were captured in the eight old-growth stands at HJAEEF, compared to only five voles in the 10 younger stands ($G = 4.73$, $P < 0.05$). Corn and Bury (1986) provide a more detailed account of these results.

Creeping Vole

Creeping voles (*Microtus oregoni*) were uncommon in closed-canopy stands (fig. 6), and there was no difference in abundance on either gradient. As with vagrant shrews, this species was more abundant in

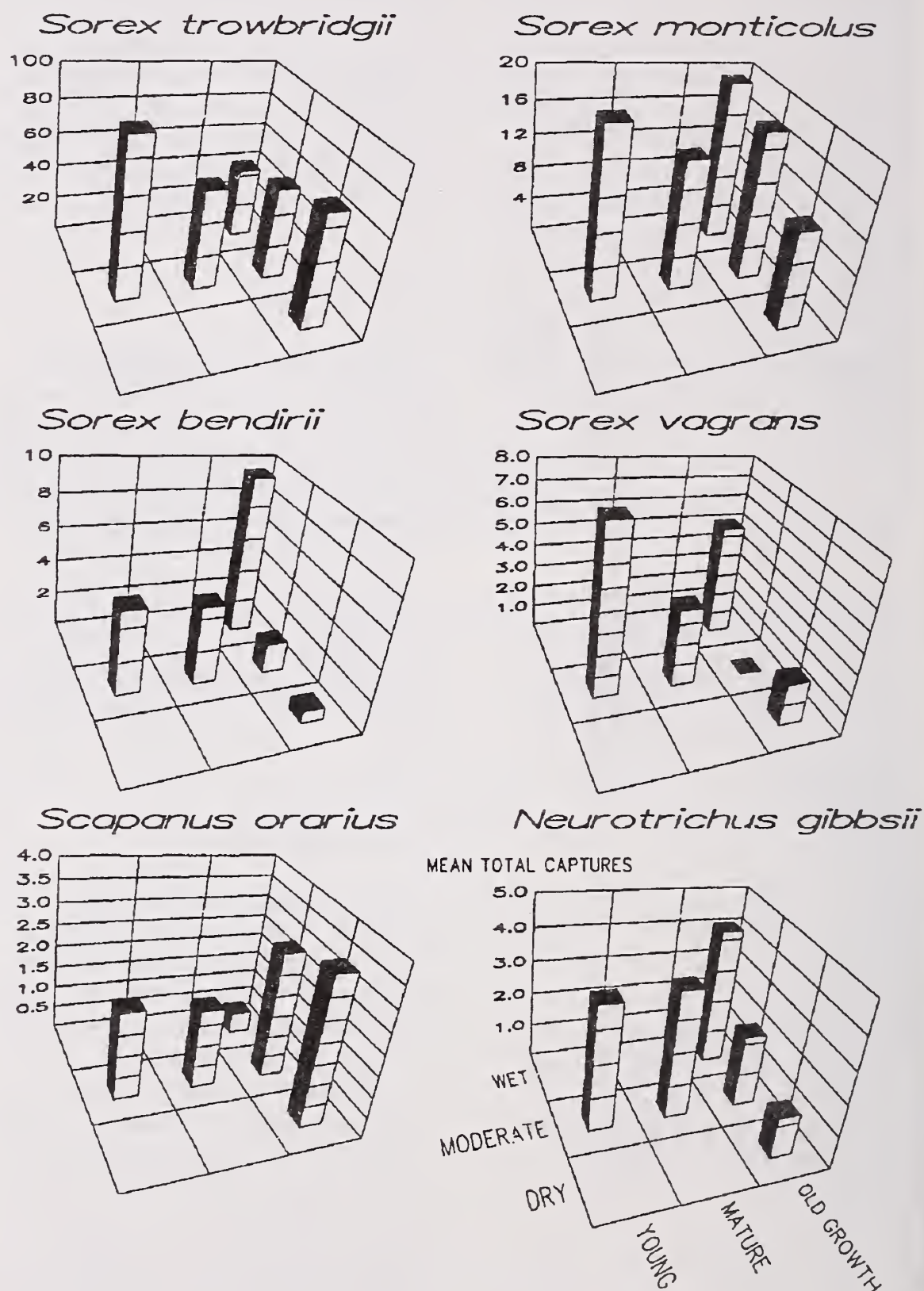


Figure 5.—Mean abundance of insectivores in closed-canopy forest stands. Data for Trowbridge's, montane, and vagrant shrews are from HJAEEF only. Pacific marsh shrews, shrew moles, and coast moles use data from all stands.

Table 3.—Significant ($P < 0.05$) Pearson correlations of insectivore abundance and stand structure and vegetation variables. See appendix B for descriptions of the variables.

Species	Positive		Negative	
	Variable	r	Variable	r
Trowbridge's Shrew ($n = 17-18$)	TOTBA	0.59	HERB	-0.75
	LNDC45	0.59	GRASS	-0.70
	MDBH	0.57	LBDC12	-0.53
	LITTER	0.49		
Montane Shrew ($n = 17-18$)	MDBH	0.51	GRASS	-0.52
Vagrant Shrew ($n = 17-18$)			LNDC12	-0.47
			LNDC45	-0.55
			MOSS	-0.50
			SLOPE	-0.51
Pacific Marsh Shrew ($n = 28-30$)	LITTER	0.41	LITTER	-0.50
	TOTDEN	0.41	LNDC12	-0.50
	MDBH	0.44	SLOPE	-0.37
	LBDC45	0.40		
Coast Mole ($n = 28-30$)	DECTR	0.52	LNDC3	-0.43
			LNDC3	-0.43

clearcuts. Reflecting this, creeping vole abundance was positively correlated with percent cover by grasses and negatively correlated with several "forest" variables: number and biomass of decayed logs, density, basal area and d.b.h. of live trees, and litter depth.

Deer Mouse

Although pitfall traps are not as effective for catching deer mice as snap traps (Williams and Braun 1983, Bury and Corn 1987), we caught moderate numbers of this species, particularly at WREF (table 2). Deer mice were most abundant in OGM stands and least abundant in OGW and young stands. Differences were not significant on either the chronosequence or the moisture gradient. Deer mouse abundance was negatively correlated with percent of coarse fragments in the soil.

Clearcuts Versus Forests

Pitfall arrays were installed in five clearcuts, three at HJAEF and two at WREF. We compared the relative abundance of several of the common small mammals in clearcuts and young stands (fig. 7). Trowbridge's, montane, and vagrant shrews were compared only for the three clearcuts and four young stands at HJAEF.

Southern and western red-backed voles were virtually absent from clearcuts, while creeping voles were more than six times more abundant in clearcuts than in young stands. Most insectivores were two to six times more abundant in young stands, but vagrant shrews were most abundant in clearcuts. Much of the difference in the relative abundance of vagrant shrews is due to their great abundance in clearcut #391 at HJAEF (table 1). Only one vagrant shrew was captured at each of the other clearcuts at HJAEF. Although roughly estimated, vagrant

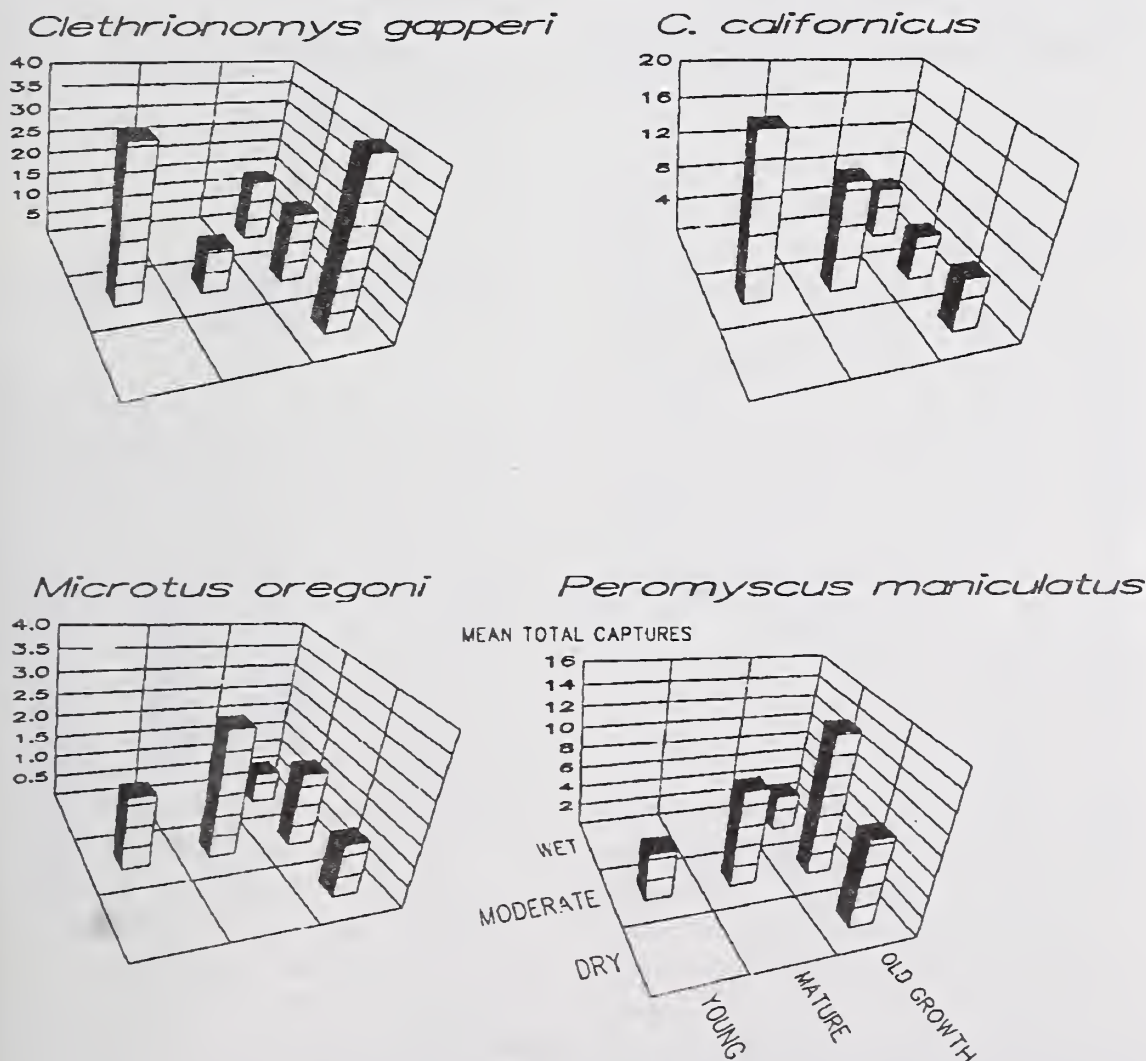


Figure 6.—Mean abundance of rodents in closed-canopy forest stands. Data from all stands were used.

shrews were the most common small mammal at both of the clearcuts at WREF. Deer mice were about three times more abundant in clearcuts than in young stands. A few pocket gophers (*Thomomys mazama* at HJAEF, *T. talpoides* at WREF) were captured and are not depicted in figure 7. Most pocket gophers (20/28) were captured in clearcuts; none were captured in old growth.

DISCUSSION

Old-Growth Species

Answering the question of if a species is dependent on old-growth forest for critical habitat is complex, incorporating several aspects of ecology and needs to account for temporal and random variation (Carey 1984). Also, abundance of individual species within a specific region depend not only on the multidimensional niche, but on the geographic distribution of each species (Brown, 1984). The community ecology studies of the Old-Growth Program were not intended to provide definite answers on old-growth dependencies, but rather the results were to be used as guides for designing species-specific research (Ruggiero and Carey 1984). Our results are based on one season's data and must be interpreted cautiously, but they are useful for comparison with other studies and for suggesting new research.

Only one small mammal, the red tree vole, displayed a significant association with old-growth stands, and the sample size for it was small. Additional captures of this species in the Oregon Coast Range in 1984-1985 were almost exclusively in old-growth forests (Corn and Bury, unpublished data). Recent studies of vertebrates across a similar chronosequence of Douglas-fir forests in northern California (Raphael 1984, this volume, Raphael and Barrett 1984) found significant positive correlations between abundance of sev-

eral species and stand age: Trowbridge's shrews, Pacific shrews (*Sorex pacificus*), coast moles, shrew moles, Allen's chipmunks (*Tamias senex*),

Townsend's chipmunks (*T. townsendii*), Douglas' squirrels (*Tamiasciurus douglasii*), dusky-footed woodrats (*Neotoma fuscipes*), deer

Table 4.—Significant ($P < 0.05$) Pearson correlations of rodent abundance and stand structure and vegetation variables. See appendix B for descriptions of the variables.

Species	Positive		Negative	
	Variable	<i>r</i>	Variable	<i>r</i>
Western Red-backed Vole (<i>n</i> = 17-18)	TOTBA	0.66	GRASS	-0.54
	MDBH	0.56	TRASPECT	-0.51
	EGSHR	0.48	LBDC12	-0.53
Southern red-backed Vole (<i>n</i> = 11-12)	TOTDEN	0.78	GRASS	-0.81
	TOTBA	0.70		
	MDBH	0.71		
Creeping Vole (<i>n</i> = 28-30)	GRASS	0.51	LNDC45	-0.58
			LBDC45	-0.43
			MDBH	-0.52
			TOTDEN	-0.40
			TOTBA	-0.49
			LITTER	-0.62
			TOTCF	-0.36
Deer Mouse (<i>n</i> = 28-30)				

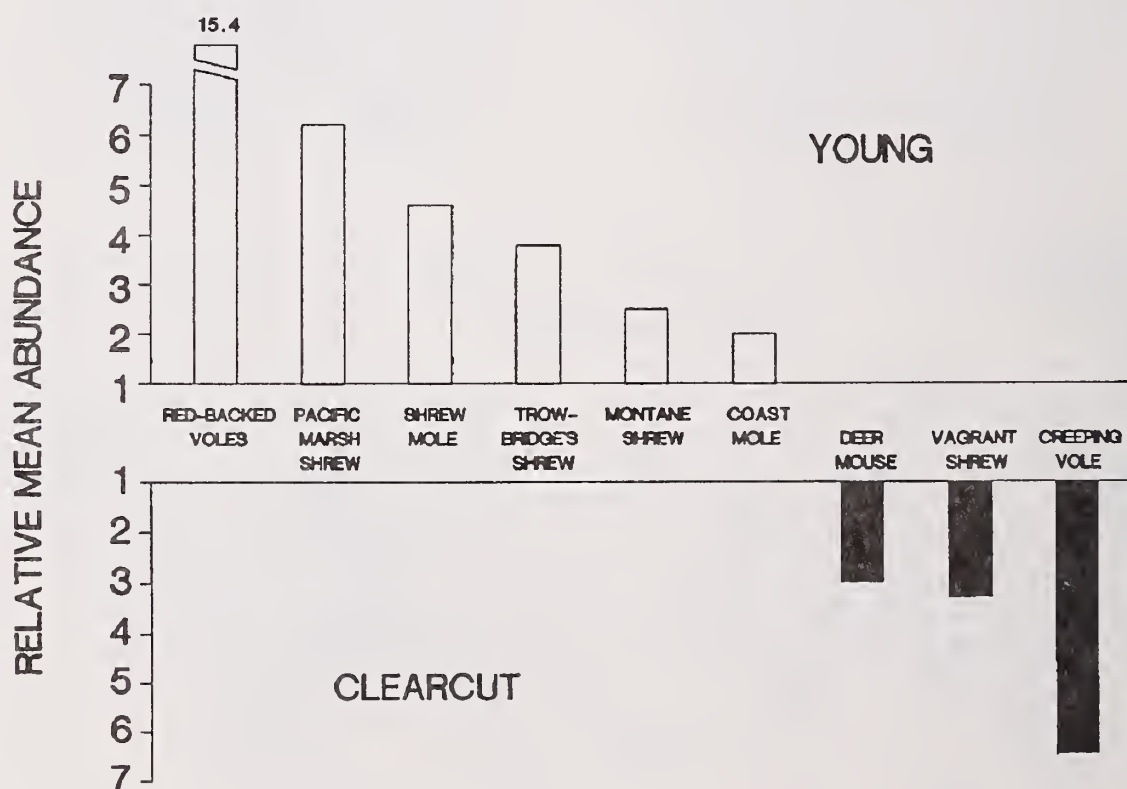


Figure 7.—Relative mean abundance of small mammals in young stands and clearcuts. Species more abundant in young stands are above the horizontal, species more abundant in clearcuts below. Values are the greater mean abundance divided by the lesser, so, for example, red-backed voles were 15.4 times more abundant in young stands than in clearcuts.

mice, western red-backed voles, and fishers (*Martes pennanti*). Many of these correlations were not strong, however, with most species represented in the youngest forest stages. Mean species richness was about 10 in all forest age classes. Analysis of the similarity of species composition showed little difference on the chronosequence (Raphael 1984). This is very similar to our results and suggests that old-growth forests do not harbor unique communities of small mammals.

Anthony et al. (1987) snaptrapped small mammals in riparian zones of old-growth, mature, and young stands at HJAEF in 1983. They found greater abundance of deer mice in old-growth stands, but Pacific shrews (*S. pacificus*) were evenly distributed. They trapped 14 other species, though none in sufficient numbers to analyze. Although both Anthony et al. (1987) and Raphael (1984) found more deer mice in older forests, this species is ubiquitous and reaches its highest densities in the Pacific Northwest in clearcuts (see below).

Small Mammals in Managed Forests

Most studies of habitat relations of small mammals in the Pacific Northwest have compared clearcuts to forested stands. Although there is considerable variation among studies, general trends are similar, likely related to the variety of factors examined (time since logging, burned, unburned, herbicides applied, etc.). Populations of deer mice, creeping voles, and Townsend's chipmunks increase after logging, while red-backed voles and Trowbridge's shrews decline (Anthony and Morrison 1985, Gashwiler 1959 1970, Hooven and Black 1976, Sullivan and Krebs 1980, Raphael, this volume, Tevis 1956). Red-backed voles are probably most affected by clearcutting. Western red-backed voles are

obligate fungivores, and their food supply disappears after clearcutting (Maser et al. 1978, Ure and Maser 1982). Gunther et al. (1983) found southern red-backed voles to be the most common animals on the clearcuts they trapped, but they trapped only three months after logging and probably were sampling a residual population. Also, this species is less dependent on fungi (Ure and Maser 1982) and might be able to persist for a time after logging.

Other studies have not noted the increase of vagrant shrews in clearcuts that we observed. Several factors might be involved, including random variation. Although mean abundance was high, vagrant shrews were rare (one capture each) on two of our five clearcuts. Other studies probably underestimated shrew abundance, because they used either snap or live traps. Also, some investigators might have followed Findley (1955) and considered montane and vagrant shrews to be the same species.

Changes in small mammal communities after logging can be dramatic, but clearcuts per se might not be the main factor influencing species diversity in managed forest landscapes in the Pacific Northwest. In a managed forest with a 90-year rotation, about 30% of the area will be in clearcuts and young plantations lacking canopy closure. The remaining 70% of the landscape will be in stands 30-90 years old that have closed forest canopies. The habitat characteristics of these forest plantations will be a major determinant of biological diversity in managed lands. For example, the extensive logging of low-elevation old-growth forests in Oregon has probably eliminated much of the habitat of red tree voles. The giant Douglas-fir trees, which seem to be preferred as nest sites, will not occur in managed forests. Meanwhile, the heather vole (*Phenacomys intermedius*), a species of alpine meadows, might be benefiting from increased logging of high-

elevation forests (Corn and Bury 1988).

Although we have found few differences between old-growth and younger naturally regenerated forests for small mammals or the herpetofauna (Bury and Corn, this volume), the same probably cannot be said for comparisons of old-growth to managed forests. Our analysis of habitat variables revealed that abundance of several species was correlated with habitat features that would be absent or greatly reduced in managed forests. Aside from large trees, CWD is the primary component of old growth that is eliminated by current forestry practices (Harris et al. 1982, Spies et al. in press). CWD is correlated to abundance of shrews (this study), salamanders (Bury and Corn, this volume, Raphael 1984), and probably is required habitat for red-backed voles (Maser and Trappe 1984). Bury and Corn (this volume) provide further discussion of the role of CWD as wildlife habitat.

Research Needs

These types of community ecology studies provided baseline data on nongame wildlife in naturally regenerated forests of the Pacific Northwest. For example, we can use the data on abundance and the correlations with habitat variables to begin classifying species as to their degree of rarity (Rabinowitz et al. 1986). Species with small geographic distributions, restricted habitat specificity, and small local populations (e.g., red tree voles, Pacific marsh shrews) are likely to be affected by habitat alteration. Species with large populations, broad habitat specificity, and either large (deer mice) or small (Trowbridge's shrews) geographic distributions, are less likely to be affected by forest management.

Our study does not address changes in habitats in managed forests stands or the effects of forest fragmentation as remaining old

growth is harvested. Further studies of small mammals should emphasize managed stands and managed landscapes.

Even with the creation of old-growth habitat areas on National Forests, most of the landscape will probably be in plantations less than 100 years old. Research needs to be focused on the degree of loss of diversity in these managed forests and evaluate silvicultural options for maintaining or enhancing habitat structure.

Thus far, there is little evidence that small mammal populations in Douglas-fir forests are strongly influenced by stand size or amount of insularization (Raphael 1984, Rosenberg and Raphael 1986). As these authors point out, however, forest fragmentation in western coniferous forests might not have advanced far enough or existed long enough for effects to be observed. Conversely, forest fragmentation in the Pacific Northwest is not usually conversion of forest to farmland or urban areas as is the case in other temperate regions (e.g., Wilcove et al. 1986, Askins et al. 1987, Dickman 1987). Rather, it results in the replacement of one forest habitat with another. Patches of old growth in a managed forest are not strict analogs of oceanic islands or isolated mountain tops (Harris 1984), so the ability of forest-floor small mammals to maintain populations in managed forests is dependent on habitat availability after logging.

Our results indicate that some "old-growth species" are found in younger stands, but the proximity of old growth to younger forest might partly explain their occurrence. The effect of stand size, shape, edge, and juxtaposition on small mammal populations needs attention. Where old growth and other habitat areas are set aside to maintain biological diversity in intensively managed landscapes, the long-term viability of these habitats and their vertebrate populations needs to be monitored.

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Table A2.—Ages, elevations, and locations of 12 stands in Washington. Locations are distances (km) from Carson, Skamania Co.

Stand	Type	Age (yr)	Elev. (m)	Location
14	OGW	375	520	17.7 N, 16.9 W
12	OGM	450	485	6.4 N, 11.3 W
21	OGM	375	440	17.2 N, 14.0 W
20	OGM	375	480	11.3 N, 11.9 W
31	OGD	375	670	18.5 N, 16.5 W
41	Mature	105	485	19.3 N, 13.7 W
42	Mature	140	500	13.7 N, 2.4 W
50	Mature	130	610	16.0 N, 2.1 W
60	Young	65	475	13.5 N, 12.1 W
61	Young	65	640	8.1 N, 6.3 W
70	Clearcut	5	535	11.3 N, 13.4 W
71	Clearcut	5	730	16.9 N, 7.2 W

Table B1.—Stand structural and vegetation variables.

Variable name	Description
SLOPE	Percent slope
TRASPECT	Transformed aspect
LNDC12	Number of logs per ha, decay class 1 and 2
LNDC3	Number of logs per ha, decay class 3
LNDC45	Number of logs per ha, decay class 4 and 5
LNDM1	Number of logs per ha, <30cm diameter
LNDM2	Number of logs per ha, >30cm and <60 cm
LNDM3	Number of logs per ha, >60 cm
LBDC12	Biomass (1,000 kg per ha) of logs, class 1 and 2
LBDC3	Biomass (1,000 kg per ha) of logs, class 3
LBDC45	Biomass (1,000 kg per ha) of logs, class 4 and 5
MDBH	Mean d.b.h. (cm) in stand
TOTDEN	Density of live trees (number per ha)
TOTBA	Basal area of live trees (m ² per ha)
LITTER	Litter depth (01 + 02 horizons; cm)
TOTCF	Volume (%) of coarse fragments in soil
MOSS	% cover by mosses
FERN	% cover by ferns
GRASS	% cover by grasses
HERB	% cover by herbaceous vegetation
EGSHR	% cover by evergreen shrubs
DESHR	% cover by deciduous shrubs
EVGTR	% cover by evergreen trees
DECTR	% cover by deciduous trees

Table A1.—Ages, elevations, and locations of 18 stands in Oregon. Locations are distances (km) from McKenzie Bridge.

Stand	Type	Age (yr)	Elev. (m)	Location
15	OGW	450	795	Linn Co., 9.2 N, 1.2 W
03	OGW	450	815	Lane Co., 6.4 N, 0.6 E
24	OGW	450	860	Lane Co., 6.0 N, 0.6 E
02	OGM	450	560	Lane Co., 4.6 N, 6.5 W
17	OGM	450	790	Lane Co., 6.6 N, 0.3 W
33	OGD	200	670	Lane Co., 6.0 N, 7.5 E
25	OGD	195	500	Lane Co., 2.4 N, 7.5 W
29	OGD	200	700	Lane Co., 2.6 S
11	Mature	140	670	Lane Co., 5.4 S, 8.8 E
35	Mature	130	900	Linn Co., 10.5 N, 1.0 W
42	Mature	150	1030	Lane Co., 3.1 N, 3.0 W
39	Young	76	1050	Lane Co., 4.4 S, 14.3 E
47	Young	50	1110	Lane Co., 3.3 N, 2.4 W
48	Young	69	1075	Linn Co., 13.2 N, 0.8 E
75	Young	30	560	Lane Co., 1.6 S, 5.2 W
55	Clearcut	9	830	Lane Co., 2.8 N, 6.6 W
291	Clearcut	5	690	Lane Co., 2.6 S, 1.4 E
391	Clearcut	5	1100	Lane Co., 3.8 S, 14.8 E

Evaluation of Small Mammals as Ecological Indicators of Old-Growth Conditions¹

Kirk A. Nordyke² and Steven W. Buskirk³

Recent emphasis in forest management has been placed on an integrated multiple-benefit approach to land and resource planning and management (Salwasser et al. 1982). The National Forest Management Act (NFMA) was enacted in 1976 to establish revised goals for the USDA Forest Service. NFMA regulations require that detailed plans be developed and implemented in each national forest. A specific goal is to manage wildlife and fish habitats to maintain viable populations of all existing native vertebrate species in the planning area and to maintain and improve habitats of management indicator species (MIS) (36 CFR 219.19). In addition, population trends of MIS are to be monitored and relationships of those trends to habitat changes must be determined (36 CFR 219.19[a][6]).

Ecological indicator species comprise one category of MIS and were defined for management purposes as "...plant or animal species selected because their population changes are

believed to indicate the effects of management activities on other species of selected major biological communities or on water quality" (36 CFR 219.19[a][1]). Ecological indicators should have a high degree of sensitivity to perturbation and be representative of habitat needs of other species (Patton 1987). Thus, population responses of an ecological indicator species to habitat perturbations should reflect similar, yet less severe, responses in more tolerant species (Graul and Miller 1984). Ecological indicators should be easily monitored to achieve realistic goals.

Compliance with the monitoring requirements of NFMA presents a major challenge to national forest management because costs may be high and because methods are still being developed (Verner 1983). The challenge is most pressing in old-growth forests: this important habitat is disappearing at an alarming rate and vertebrate populations dependent on old-growth features are declining (Harris 1984). NFMA guidelines mandate that old-growth be a significant element in the diversity of forest conditions. To accomplish this, old-growth and associated fauna must be characterized and monitored to determine that management practices will not impair their productivity (Juday 1978).

Of 22 species selected as ecological indicator species for the Medicine Bow National Forest (MBNF), Gapper's red-backed vole (*Clethrionomys*

Abstract.—The use of small mammals as ecological indicators of old-growth conditions was evaluated from trapping studies conducted in forest stands reflecting a range of old-growth conditions in southeastern Wyoming. The relationship between abundance of *Clethrionomys gapperi* and old-growth conditions was expressed in a quadratic function. *Tamias minimus* and *Peromyscus maniculatus* were negatively correlated with old-growth conditions. *C. gapperi* is the most likely candidate for a small mammal ecological indicator of old-growth conditions in spruce-fir stands.

gapperi) is the only small mammal ecological indicator for old-growth conditions (USDA Forest Service 1985). Old-growth forests represent optimal habitat for *C. gapperi* (Jerry 1984). Limiting factors to habitat use by *C. gapperi* may include requirements for water (Getz 1968, Merritt 1981) and log cover (Tevis 1956). Old-growth generally exhibits more mesic conditions than other forest habitats. Logs provide cover from predators and weather (Maser et al. 1979), pathways into new habitats (Franklin et al. 1981), and mesic sites for fungal growth (Maser and Trappe 1984). The importance of fungi as a food for *C. gapperi* has only recently been recognized (Martell 1981, Maser et al. 1978a). Mesic conditions of old-growth stands favor the occurrence of fungi (Maser et al. 1978b).

The indicator species concept was adopted by the Forest Service in the late 1970s, but its viability as a monitoring approach has not been investigated. Certain parameters of *C. gapperi* populations were assumed to reflect changes in old-growth conditions that result from management activity. This paper describes a study investigating the application of the indicator species concept to old-growth management. Our objective was to evaluate the responses of small mammal populations to a range of old-growth conditions. Specifically, we investigated whether abundance of *C. gapperi* was related to old-growth condition.

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Study Area and Methods

Our study area in the Snowy Range included upper montane (2300-2750 m) and subalpine (2750 m-timberline) zones. Lodgepole pine (*Pinus contorta*) was the dominant overstory species in the montane zone; it also dominated south slopes and ridge tops at higher elevations (Romme and Knight 1981). Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) were generally co-dominant in the subalpine zone (Alexander 1974). Engelmann spruce and subalpine fir are climax species (Romme and Knight 1981) and often develop old-growth conditions. Old-growth conditions in lodgepole-dominated stands are less common due to a shorter fire interval and a slower rate of succession (Romme and Knight 1981). Understory vegetation was sparse and generally consisted of common juniper (*Juniperus communis*) and broom huckleberry (*Vaccinium scoparium*).

Field studies were conducted in the MBNF (fig. 1) from June to September of 1986 and 1987. We established eight study plots in spruce-fir stands reflecting a range of old-growth conditions. Because plots were located on both the east and west slopes, a paired design was used to control for the effects of major relief. A 1.42-ha trap grid with 80 Museum Special snap-traps (8 by 10 pattern with 15-m intervals) was located on each plot. In 1987, four ad-

ditional grids were located on plots dominated by lodgepole pine. Snap-traps were baited with peanut butter and oatmeal. Beginning in July 1986, we trapped each grid for three consecutive nights and checked traps daily in early morning. If rainfall caused the release of snap-trap mechanisms, trapping effort was extended by as many nights as it rained (table 1).

In 1987, we rated the old-growth condition of our study plots with the old-growth scorecard developed specifically for the MBNF (Marquardt

1984) (table 1). The scorecard is completed subjectively by Forest Service personnel and is based on structural characteristics of stands. Structural characteristics that define old-growth stands in the MBNF include trees with large diameters, long-lived dominant species (i.e., Engelmann spruce and subalpine fir), a multi-storied stand structure, dense canopies, multiple species, woody debris on the forest floor, and standing snags (Marquardt 1984). The scorecard incorporates sub-scores for each of these structural characteristics to

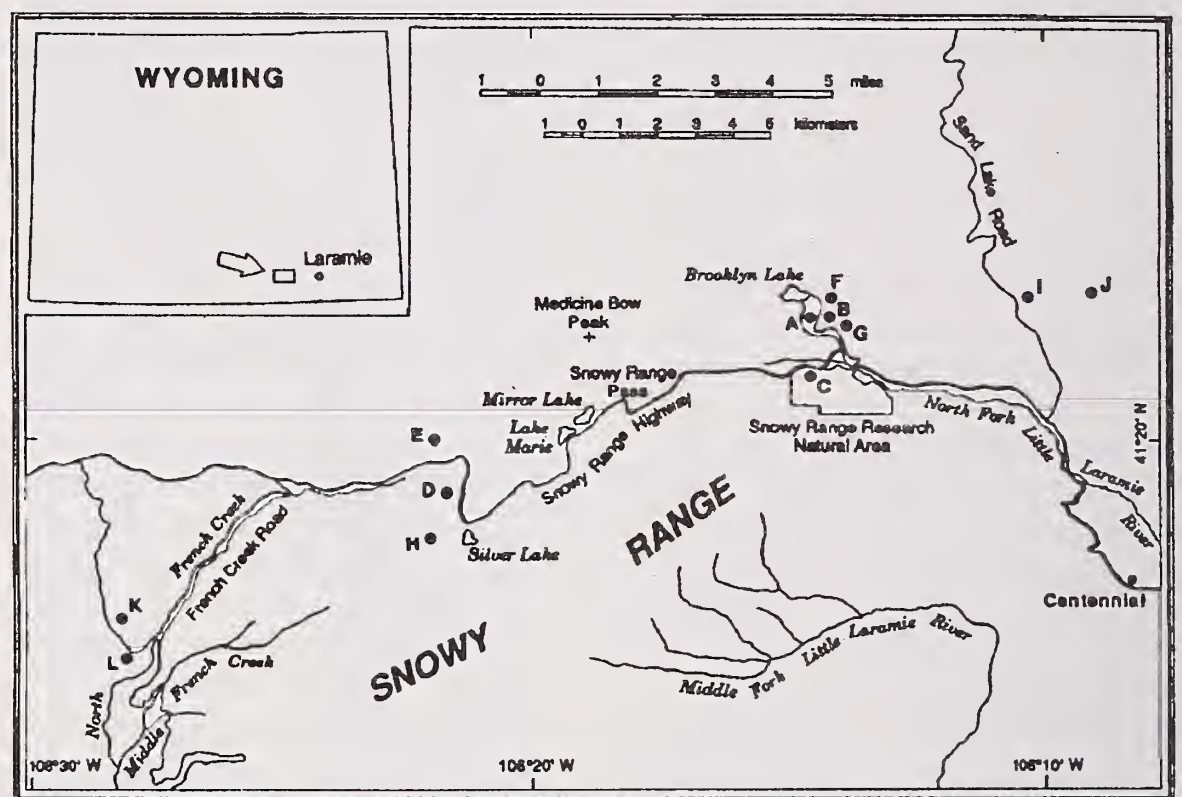


Figure 1.—Map of the study area in the Medicine Bow National Forest of southeastern Wyoming, about 65 km west of Laramie. Twelve study plots (A-L) were established in 1986 and 1987 for intensive trapping and habitat characterizations.

Table 1.—Information collected from 12 study plots in the Medicine Bow National Forest of southeastern Wyoming in 1986 and 1987.

Characteristic	Study plot											
	A	B	C	D	E	F	G	H	I	J	K	L
USFS location site	20130703	20130307	20130405	20540334	20540420	20130308	20130310	20810323	20181015	20180910	20490707	20550326
Dominant overstory	spruce fir	spruce	spruce fir	spruce fir	spruce fir	spruce fir	spruce fir	spruce fir	lodgepole	lodgepole	lodgepole	lodgepole
Old-growth rating	51	35	48	44	50	37	40	41	25	22	22	19
Trapping effort 1986 (# trap nights)	240	240	240	320	240	400	240	240	0	0	0	0
	320	320	320	320	240	240	240	240	240	240	240	240

achieve an overall old-growth rating, ranging from 0 to 60.

We quantitatively determined sub-scores for characteristics we believed were most important to meeting habitat needs of *C. gapperi*. Log density was estimated with the point-quarter distance method (25 sampling points) and the diameter of each log sampled (100 logs were sampled) was measured to determine the mean log diameter.

Data analyses were performed with the SPSS computer package (Nie et al. 1975). Analyses involved linear and quadratic correlation tests between small mammal abundance

(as inferred from capture success) and old-growth ratings. While interested primarily in the responses of *C. gapperi* populations, we also evaluated the responses of other small mammal species that were captured.

Results and Discussion

A total of 695 small mammals were captured in 5,360 trap nights (TN). In decreasing abundance, these were *C. gapperi*, *Tamias minimus*, *Sorex* spp., *Peromyscus maniculatus*, *Phenacomys intermedius*, *Sorex cinereus*, *S. monticolus*, and *Microtus longicaudus*. Only captures of *C. gapperi* and *T. minimus* were frequent enough to provide data for analysis both years; captures of *P. maniculatus* were adequate only in 1987. Other species were rarely captured.

Temporal Fluctuations in Abundance

Mean capture success increased three-fold from 1986 (5.6/100TN) to 1987 (18.0/100TN). Capture success of *C. gapperi* is representative of this variation (fig. 2). Natural fluctuations in small mammal abundance are well documented (Krebs and Myers 1974, Vaughan 1969). Such fluctuations are a major source of confounding variation and hinder the ability of managers to monitor populations for changes that result from human-induced disturbance. Because of this temporal variation in abundance, we separated the data for analysis.

Association of *C. gapperi* with Old-Growth Conditions

In 1986, the abundance of *C. gapperi* was weakly correlated linearly with old-growth ratings ($r = 0.62$, $P = 0.097$). However, this result represented only the range of old-growth conditions found in spruce-fir stands (scores ranged from 35 to 51). Four

lodgepole pine study plots, which rated lowest on the old-growth scorecard and provided a greater range of ratings (19-51), were added in 1987. A more complete pattern emerged: *C. gapperi* was most abundant in the lowest-scoring lodgepole study plot, decreased in the remaining lodgepole plots, further decreased to a minimum in the mid-range spruce-fir plots, and then increased in abundance with increasing old-growth condition in the remaining spruce-fir plots. A quadratic correlation model best explained the relationship between abundance of *C. gapperi* and old-growth ratings in 1987 ($r = 0.81$, $P = 0.007$; fig. 3).

The highly significant quadratic function that described the relationship between abundance of *C. gapperi* and old-growth rating in 1987 should be interpreted separately for the lodgepole pine and spruce-fir segments. In spruce-fir plots, the relationship was positive ($r = 0.89$, $P = 0.003$), as it was (suggestively) in 1986. However, a comparison of *C. gapperi* abundance in spruce-fir plots between 1986 and 1987 was not significant ($r = 0.43$, $P = 0.290$). This indicated that the spruce-fir plots supporting high densities of *C. gapperi* in 1986 were not the same plots supporting high densities in 1987. In lodgepole plots (1987 only), abundance of *C. gapperi* was not significantly correlated with old-growth rating ($r = -0.88$, $P = 0.116$). Therefore, we are not confident in the results from the lodgepole plots, but an interpretation is warranted. The abundance of *C. gapperi* in both seral phases (lodgepole and spruce-fir) was strongly influenced by the abundance of woody debris (particularly logs) on the forest floor. However, these two stand types differ markedly in terms of the source, size and likely persistence of logs.

In spruce-fir plots, logs were large (mean diameter was 31.0 cm) and were recruited through the natural processes of windthrow and snag decay. Log size and biomass are

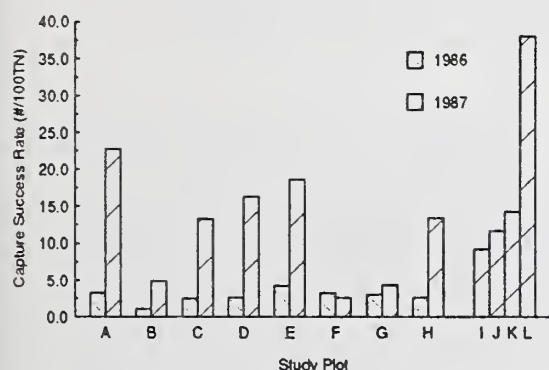


Figure 2.—Capture success of *Clethrionomys gapperi* in 12 study plots in the Medicine Bow National Forest of southeastern Wyoming in 1986 and 1987. Temporal variation in abundance was extreme in five of the eight spruce-fir plots sampled both years. Plots I-L were dominated by lodgepole pine and were sampled only in 1987.

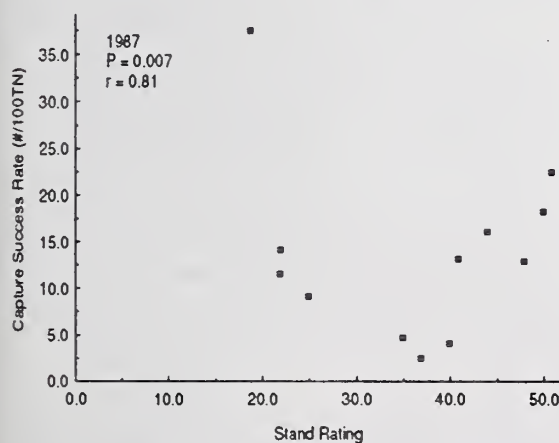


Figure 3.—Capture success of *Clethrionomys gapperi* in the Medicine Bow National Forest of southeastern Wyoming in 1987 as a function of old-growth ratings. This relationship is best explained by a quadratic correlation. Darkened data points represent lodgepole-dominated study plots; open data points represent spruce-fir-dominated study plots.

greater in older forests than in younger forests (Franklin et al. 1981). Thus, availability and size of logs increase with time in young spruce-fir stands, and we believe that this increase was primarily responsible for the relationship we found between abundance of *C. gapperi* and old-growth rating of spruce-fir plots. In lodgepole plots, logs were smaller than in spruce-fir plots (mean diameter was 22.7 cm; $t = 7.93$, $P = 0.004$) and were recruited almost entirely by thinning. One lodgepole plot (plot L, in site 205503-26, table 1) had been thinned 13 months before we sampled it and had a high density of logs and the greatest abundance of *C. gapperi*. This single plot overwhelmingly influenced the lodgepole phase of the quadratic function.

Lodgepole stands do not thin well naturally (Alexander 1974), so log recruitment rates and densities are generally low. We predict that, because they are larger and are recruited at a less variable rate, logs in spruce-fir stands are more persistent over time than are logs in lodgepole stands. Kirkland (1977) and Martell and Radvanyi (1977) found high densities of *C. gapperi* in clearcuts one year after logging spruce forests. Three years after logging, Martell and Radvanyi found that *C. gapperi* had become rare. Gunther et al. (1983) attributed the abundance of *C. gapperi* in clearcuts to high ground cover created by felled trees and slash and to an abundant food supply of lichens.

Interpretation of *C. gapperi* abundance as an indication of old-growth condition must be undertaken with caution. *C. gapperi* appears to respond to natural processes of log accumulation; however, *C. gapperi* populations also appear to respond to accumulation of woody debris resulting from management actions. Stand thinning is more common in lodgepole than in spruce-fir stands in the MBNF (T. Cartwright, pers. comm.), so use of *C. gapperi* as an indicator of old-growth conditions of

spruce-fir stands appears less likely to be confounded by this factor.

Association of *T. minimus* and *P. maniculatus* with Old-Growth Conditions

The broad habitat affinities of these two species are well documented (Armstrong 1977). In forested habitats, they are associated with early successional stages (Martell 1984). In our study, *T. minimus* abundance decreased with increasing old-growth rating in 1986 ($r = -0.71$, $P = 0.046$; fig. 4), but the correlation was based on a narrow range of ratings so that its reliability is questionable. Vaughan (1974) noted this species' dependence on stumps and rocks for lookout points. Certain structural features that characterize old-growth conditions (e.g., restricted average sight distance) are inconsistent with the open habitat requirements of *T. minimus*. There was no significant correlation in 1987. Given the high population levels that year, limited resources in preferred habitat may have caused *T. minimus* to disperse into less preferred habitat.

Abundance of *P. maniculatus* decreased with increasing old-growth rating in 1987 ($r = -0.60$, $P = 0.039$; fig. 5), but the correlation was driven by one data point (study plot L, table 1). The abundance of *P. maniculatus* has been shown to increase with understory vegetation (Tevis 1956). If this is due to an affinity for cover, then the conditions present in study plot L may explain the high numbers of *P. maniculatus* found there. If the data point is excluded from the analysis, the result supports the broad habitat distributions *P. maniculatus* is known to exhibit.

Conclusions

We found that abundance of *C. gapperi* was correlated with old-growth ratings in spruce-fir stands, and at-

tribute that correlation primarily to the log component of the old-growth rating. *C. gapperi* was strongly correlated with old-growth conditions in spruce-fir and may be predictive of old-growth condition in that stand type. However, *C. gapperi* appears to respond to logs recruited from management activities, and caution should be used in interpreting abundance data.

Our results neither support nor refute the assumption that *C. gapperi* represents the habitat needs of other species. Alternative monitoring approaches may have utility in forest management. These include guild-indicator species, whole-guild, and community-based monitoring schemes.

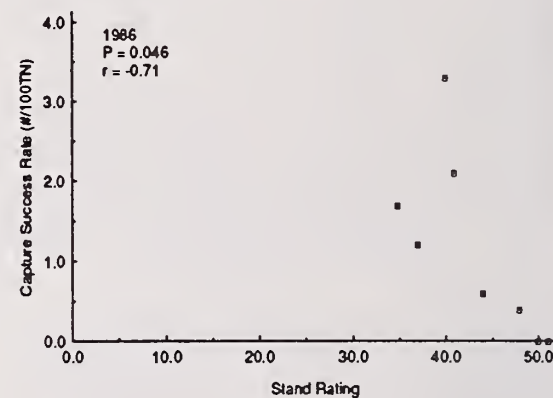


Figure 4.—Capture success of *Tamias minimus* in the Medicine Bow National Forest of southeastern Wyoming in 1986 as a function of old-growth ratings in spruce-fir-dominated study plots.

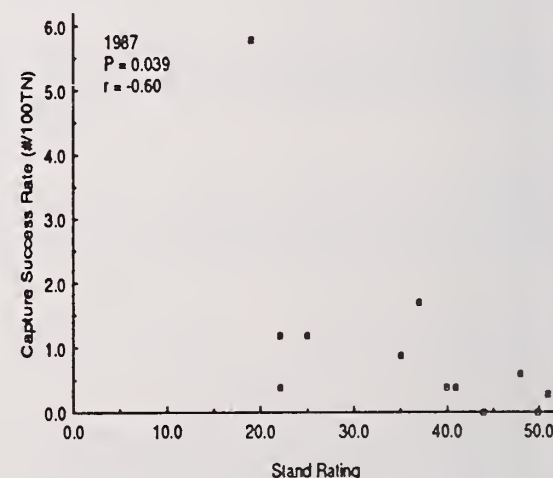


Figure 5.—Capture success of *Peromyscus maniculatus* in the Medicine Bow National Forest of southeastern Wyoming in 1987 as a function of old-growth ratings. Darkened data points represent lodgepole-dominated study plots; open data points represent spruce-fir-dominated study plots.

Tamias minimus and *P. maniculatus* populations responded in a manner consistent with their habitat affinities. Thus, *C. gapperi* may be the only choice for consideration as a small mammal ecological indicator of old-growth conditions in the MBNF.

Acknowledgments

We wish to thank the USDA Forest Service, Medicine Bow National Forest, and the Wyoming Game and Fish Department for funding this project. We appreciate very constructive reviews by M. Raphael and W. Block.

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Habitat Associations of Small Mammals in a Subalpine Forest, Southeastern Wyoming¹

Martin G. Raphael²

Subalpine forests of spruce, fir, and lodgepole pine cover about 5 million ha, or 38% of forested land in the central Rocky Mountain region—more than any other forest type (Alexander 1974, USDA Forest Service 1980). Subalpine forest is harvested heavily, accounting for over 90% of total sawtimber volume in this region (USDA Forest Service 1980). These forests also are managed to produce water, and timber harvest practices have been developed that can substantially increase water yield (Troendle 1983, Swanson 1987). The Coon Creek Water Yield Augmentation Pilot Project (Bevenger and Troendle 1984, 1987) is a large-scale demonstration of the feasibility and costs/benefits of increasing water yield through specially designed clearcuts. To evaluate the response of wildlife species to such harvests, studies were initiated to describe the pre-treatment structure and composition of the vertebrate community (Raphael 1987b) and, ultimately, to compare responses of vertebrates on the treated watershed and on the unharvested control.

The present study summarizes the structure of the small mammal com-

¹Paper presented at Symposium, Management of Amphibians, Reptiles, and Small Mammals in North America (Flagstaff, AZ, July 19-21, 1988).

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Abstract.—Mammal capture rates were greatest at sites with mature timber and other old-growth attributes. Shrews (both dusky (*Sorex monticolus*) and masked (*S. cinereus*)) and southern red-backed voles (*Clethrionomys gapperi*) were much more abundant at sites dominated by spruce or fir compared to drier sites dominated by lodgepole pine. Deer mice (*Peromyscus maniculatus*), in contrast, were most abundant on drier, pine-dominated sites. The southern red-backed vole, because of its high abundance and strong association with mature forest, is a good ecological indicator of late seral conditions for forest planning purposes.

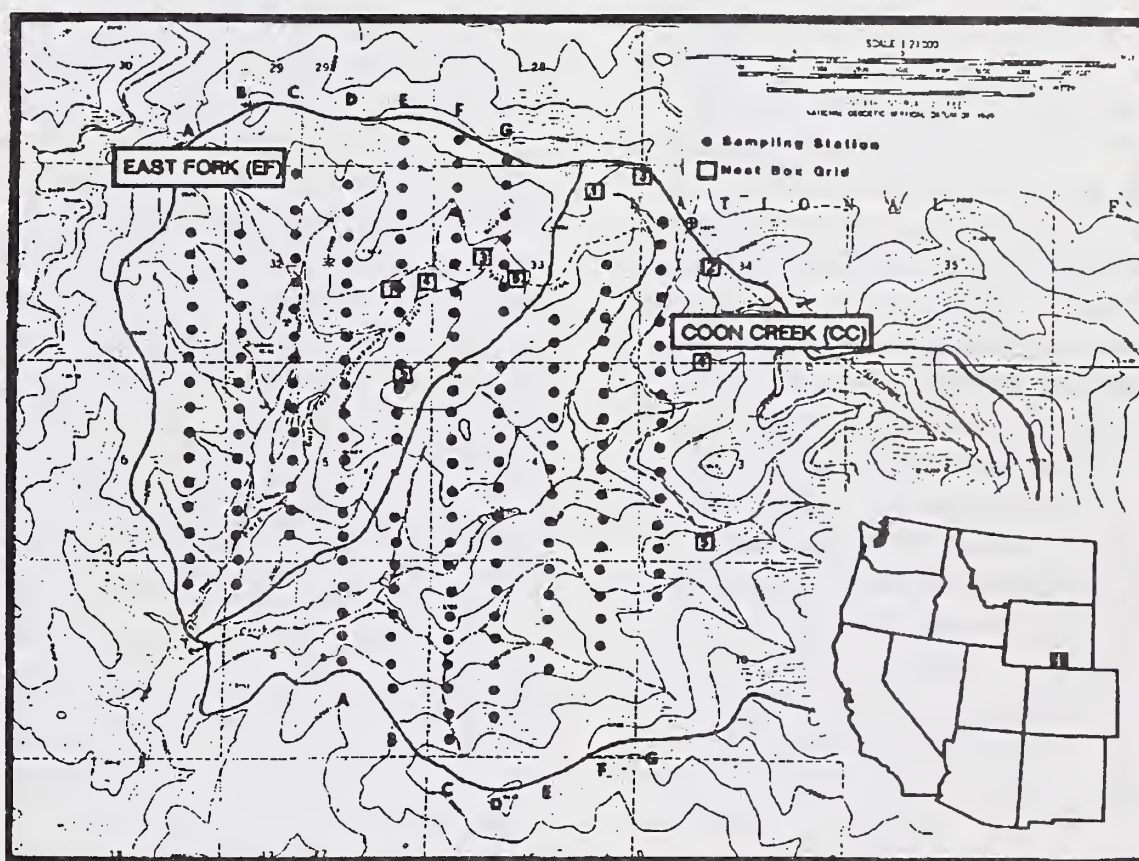


Figure 1.—Map of study area showing location of study area and distribution of trapping stations.

munity, describes habitat associations of the dominant species during the pretreatment phase of the longer term project, evaluates the efficacy of an old-growth scorecard to rate old-growth characteristics of stands, and assesses designation of mammals as ecological indicators of old-growth conditions.

STUDY AREA

Studies were conducted within two watersheds, the Upper East Fork of

the Encampment River (911 ha) and Coon Creek (1,615 ha). These adjacent watersheds are part of the Sierra Madre range of southern Wyoming, located about 25 km south of the town of Encampment (fig. 1). Elevations vary from 2,600 to 3,300 m. Soils are 50-150 cm deep and are well drained.

Mean annual precipitation is about 100 cm, 70% falling as snow that usually covers the site from late September through late June at depths of 2-4 m in winter. Forest cover is dominated by lodgepole pine (~ 60% of

land area), and a mixture of Engelmann spruce and subalpine fir. Pole stands with trees <23 cm d.b.h. occur on 24% of the two watersheds, mature stands occur on 72%, and meadows or rock outcrops cover 4%.

METHODS

Vegetation Sampling

In each watershed, 90 sampling stations were established at 200-m intervals along N-S lines that were 400 m apart (fig. 1). At each of the 180 stations, an observer measured basal area of each tree species using a 1-factor metric reloskop. Canopy cover was estimated from the average of four readings taken at cardinal directions with a spherical densiometer. Slope was measured with a clinometer and aspect was measured with a hand-held compass. All snags >20 cm d.b.h. and 1.8 m tall were counted within a 0.04-ha circular plot centered at the station; cover percentages of shrubs, forbs, grasses, rocks, litter, and bare ground were visually estimated over the same 0.04-ha plot. Hard (class 1,2) and soft [class 3,4,5 (Maser et al. 1979)] logs also were counted on each plot. Height and d.b.h. of one representative tree were measured at each station with a clinometer and metric d.b.h. tape.

All stands on each watershed were assessed by personnel of the Medicine Bow National Forest and assigned an old-growth rating based on canopy structure, d.b.h., tree height, snag size and density, and log size and density (appendix). Possible scorecard values range from 0 (no old-growth characteristics) to 60 (maximum).

Stand maps were used to associate a sampling station with the old-growth scorecard value for the stand in which the station was located. Habitat types were also assigned to each station based on classifications used by Medicine Bow National For-

est personnel. Also recorded was the presence or absence of permanent streams within 100 m of each sampling station.

Red Squirrel Counts

Three observers visited each sample station twice each year (totaling six visits/station/yr) from 13 June to 25 July 1985, 18 June to 23 July 1986, and 15 June to 17 July 1987. At each visit, the observer recorded all red squirrels seen or heard within a 100-m radius of the station center. All counts were begun within 30 minutes after sunrise; each observer visited 15

stations per day and most counts were completed before noon.

Small Mammal Trapping

To sample shrews, six pitfall traps were installed in a 2 x 3 grid (15-m spacing) centered on each station. Each pitfall trap was a 3-gal plastic bucket buried flush with the ground surface and covered by logs or bark. To capture other small mammals, two 50-cm Sherman livetraps were placed within 2 m of each pitfall station.

Mammals were trapped during late summer from 1985 to 1987 (20

Table 1.—Vegetation and stand attributes on small mammal trapping stations, estimated or measured on 0.04-ha circular plots, among habitat types¹ on a Sierra Madre forest, Wyoming.

Characteristic	Lodgepole pine			Spruce/fir	
	Unclassified (n=9)	Pole (n=36)	Mature (n=76)	Mature (n=59)	Signifi- cance ²
Basal area (m ² /ha)					
Lodgepole pine	12.1 ^B	19.2 ^A	21.3 ^A	10.6 ^B	0.01 ^W
Engelmann spruce	8.9 ^{AC}	5.2 ^A	6.3 ^A	11.9 ^C	0.01 ^W
Subalpine fir	10.7	8.6	7.4	10.2	0.18
Tree height (m)	19.9 ^{AC}	18.2 ^A	20.3 ^{BC}	21.2 ^{BC}	0.00
D.B.H. (cm)	29.8 ^{AB}	27.0 ^A	32.9 ^B	36.6 ^C	0.00
Snags/0.04 ha	2.1	1.2	2.0	2.4	0.29 ^W
Percent cover					
Shrubs and trees >2 m tall	45.3 ^{AC}	54.1 ^A	50.8 ^A	38.4 ^{BC}	0.01
Forbs	14.0	6.4	7.6	15.0	0.12 ^W
Grasses	14.8	7.4	7.6	16.4	0.18 ^W
Rocks >15 cm	0.8 ^A	4.4 ^{AB}	3.9 ^B	3.2 ^{AB}	0.00 ^W
Litter	82.0 ^{BC}	85.6 ^{AC}	82.7 ^C	73.6 ^B	0.07 ^W
Bare soil	0.4	1.0	1.2	1.8	0.30 ^W
Hard logs >20 cm diameter	0.6 ^A	1.9 ^{AB}	2.3 ^B	2.7 ^B	0.00 ^W
Soft logs >20 cm diameter	9.6	10.7	11.7	10.9	0.63 ^W
Overstory canopy	65.8	69.2	68.2	62.4	0.32 ^W
Old-growth scorecard index	19.0 ^{ABC}	29.4 ^A	34.9 ^B	41.5 ^C	0.00
Stream presence ³	22.0	25.0	38.2	37.3	0.45
Solar radiation index ⁴	0.45 ^A	0.50 ^A	0.50 ^A	0.48 ^A	0.02
Elevation (10 ³ m)	9.0 ^A	9.4 ^B	9.5 ^B	9.4 ^B	0.00 ^W

¹Letter superscripts denote results of multiple comparisons (Tukey-Kramer or Dunnett's simultaneous procedures); means with same letter did not differ. Experiment-wise error rate maintained at $\alpha = 0.05$.

²Significance of analysis of variance F-tests among habitats; W indicates that Welch's test was performed when variances were unequal.

³Percent of stations within 100 m of stream.

⁴Index of yearly solar radiation input (Frank and Lee 1966).

August through 26 September 1985, 5 August to 11 September 1986, and 4 August to 10 September 1987). Observers checked traps once daily during each of three, 10-day sampling sessions each year. Sampling sessions were separated by four days, encompassing six weeks each year. All captured specimens were identified, toe clipped, sex determined, aged, weighed, and checked for reproductive status (currently breeding or not).

Dead animals were assigned a permanent catalog number. Shrews were preserved in 70% ethanol and all other species were frozen for later identification.

Data Analysis

Total numbers of detections (red squirrels) or first captures (all other species) were calculated at each station over the 3 years. Thus, the total numbers of captures represented the results of 450 trapnights of effort at each of the 180 stations (81,000 total trapnights). Despite efforts to close

pitfall traps between sessions, some mammals were captured before the start of each 10-day session. These specimens were retained, but numbers were not included in analyses.

To assess habitat associations of the more abundant mammals, I performed a principal components analyses (with varimax rotation) using the SPSS/PC+ program package (Norusis 1988). Principal components analysis derives linear combinations of attributes (in this case vegetation characteristics as listed in table 1). All components with eigenvalues >1.0 were retained for subsequent analyses. The equations were then "solved" for each station, resulting in a set of scores that were interpreted as habitat gradients. I identified these gradients from those original habitat variables most highly correlated with the principal components scores. To relate abundance of the more abundant mammals to habitat features at each station, I performed multiple regressions of capture rates at each station (dependent variable) with the habitat gradients or principal components scores (independent variables).

To summarize patterns of co-occurrence of the more common mammal species, I performed an average-linkage-between-groups cluster analysis [UPGMA (Norusis 1988)] based upon Pearson correlations between abundances of all pairs of species among the 180 stations. Results of the cluster analysis were displayed using a dendrogram showing the relative similarities of all species. The similarity measure, for this display, was rescaled to values ranging from 0 (no similarity) to 25 (maximum similarity).

RESULTS AND DISCUSSION

Vegetation

Structure and composition of vegetation (table 1) were typical of sub-alpine forest in the central Rocky Mountains (Alexander 1974; Raphael 1987a, 1987b). Vegetation characteristics have been shown to be similar between the two watersheds (Raphael 1987b); therefore, no distinction was made between the two watersheds for this study.

Principal components analysis resulted in the creation of six synthetic habitat gradients that, together, contained 68% of the total variance from the 19 original habitat variables (table 2). I used the variables that were most highly correlated with values of each gradient to interpret the biological meanings of the gradients (table 2).

Mammals

Over the 3 years of study and over all sampling stations, observers captured 4,553 individuals of 17 small mammal species and recorded 987 detections of red squirrels (table 3). The most abundant species was the southern red-backed vole, accounting for over 50% of all captures. Other dominant species included masked shrew (15%), deer mouse

Table 2.—Habitat gradients derived from principal components analysis of 19 variables (table 1) describing vegetation structure and composition at each small mammal sampling station, Sierra Madre, Wyoming.

Gradient	Percent of variance ¹	Cumulative percent	Interpretation of habitat gradient ²
1	26.2	26.2	Greater cover of shrubs and litter; greater basal area of lodgepole pine; lower cover of herbs, grasses.
2	16.1	42.3	Greater expression of old-growth attributes; greater basal area of Engelmann spruce.
3	8.7	51.0	Upland sites with greater cover of soft logs; greater basal area of subalpine fir.
4	7.4	58.4	Lower cover of bare ground; greater canopy cover.
5	6.6	65.1	Greater cover of rocks.
6	5.6	70.7	Higher elevation sites with greater solar radiation (southerly slopes).

¹Amount of total variance (among all original variables) accounted for by each principal component.

²Interpretation based on magnitude of correlations of original variables with derived components. Descriptions indicate positive extreme of each gradient.

(15%), red squirrel, dusky shrew (6%), and chipmunks (2 species, 6%).

Specific Habitat Associations

Masked Shrew

Masked shrews were more abundant than other shrews and were captured more frequently in mature lodgepole and spruce/fir sites (table 3) with higher cover of herbs and grasses; they were less abundant on dry, south-facing sites (table 4). Their abundance at each station was modeled ($R^2 = 0.42$) by a regression that included gradients 2,1,6, and 4 (in order of their statistical significance) (table 4). Other studies (Negus and Findley 1959, Spencer and Pettus 1966, Brown 1967a, Armstrong 1977) also report this species' preference for moist sites. However, I did not find a strong association with bogs, as reported by Brown (1967a) and Spencer and Pettus (1966).

Dusky Shrew

Dusky shrews were captured in greater numbers in more moist, mature spruce/fir sites (table 3). They were most strongly associated with dense herbaceous cover and (to a lesser degree) with old-growth attributes. Unlike the masked shrew, their abundance was positively and significantly correlated with gradient 3 (moist, streamside sites; tables 2,4). Like masked shrews, they were less abundant on southerly, steeper sites. The regression model explained 41% of variance in abundance (table 4). Brown (1967a) captured this shrew in a greater variety of habitats and in drier sites than the masked shrew. Negus and Findley (1959) also reported use of a greater variety of habitats; Spencer and Pettus (1966) found dusky shrews in association with marshy habitats.

The association of this shrew with old-growth conditions has not, to my

knowledge, been previously reported.

Least Chipmunk

The abundance of least chipmunk was significantly and negatively correlated with gradient 4 (bareground) and positively correlated with gradient 6 (southerly exposure). Although

the regression was statistically significant, it explained only 5% of variance in abundance (table 4); thus, the regression model was not statistically meaningful.

Nonetheless, the associations suggested by the model, particularly the preference for open, drier slopes, are in accordance with results of other studies (e.g., Telleen 1978, Clark and Stromberg 1987).

Table 3.—Small mammal capture rates among generalized habitat types¹ in the Sierra Madre, Wyoming, 1985-1987.

Species	Total no. individuals captured	Lodgepole pine Pole (n=36)	Mature (n=76)	Spruce/fir Mature (n=59)	Sig. ²
Masked shrew (<i>Sorex cinereus</i>)	700	2.6 ^A	3.7 ^{AB}	5.0 ^B	0.01
Dusky shrew (<i>S. monticolus</i>)	253	0.6 ^A	0.8 ^A	2.7 ^B	0.01
Dwarf shrew (<i>S. nanus</i>)	2	0	0	0.03	NT
Water shrew (<i>S. palustris</i>)	7	0	0.08	0.02	NT
Pygmy shrew (<i>S. hoyi</i>)	11	0.03	0.09	0.03	NT
Least chipmunk (<i>Tamias minimus</i>)	101	0.8 ^A	0.4 ^A	0.7 ^A	0.50
Uinta chipmunk (<i>Tamias umbrinus</i>)	150	1.1 ^A	0.9 ^A	0.6 ^A	0.51
Golden-mantled ground sq. (<i>Spermophilus lateralis</i>)	11	0.06	0.11	0.02	NT
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	3987	5.8 ^A	4.7 ^A	6.0 ^A	0.23
Northern pocket gopher (<i>Thomomys talpoides</i>)	1	0	0.01	0	NT
Deer mouse (<i>Peromyscus maniculatus</i>)	696	3.3 ^A	4.2 ^A	3.5 ^A	0.31
Southern red-backed vole (<i>Clethrionomys gapperi</i>)	2,475	10.8 ^A	11.4 ^A	18.0 ^B	0.02
Heather vole (<i>Phenacomys intermedius</i>)	17	0.08	0.09	0.10	NT
Montane vole (<i>Microtus montanus</i>)	32	0.03 ^A	0.09 ^A	0.37 ^A	0.08
Long-tailed vole (<i>M. longicaudus</i>)	11	0.03	0.08	0.07	NT
House mouse (<i>Mus musculus</i>)	1	0	0	0.02	NT
Western jumping mouse (<i>Zapus princeps</i>)	80	0.1 ^A	0.4 ^B	0.7 ^B	0.00
Ermine (<i>Mustela erminea</i>)	6	0	0.05	0.02	NT

¹Values are mean capture rates (captures/450 trapnights) or mean numbers of detections (red squirrel) among habitat types for all years combined. Letter superscripts indicate results of multiple comparisons; means with same letter did not differ significantly.

²Significance from one-way analysis of variance; NT = not tested because of small sample size.

³Results are expressed as numbers of detections during call counts.

Uinta Chipmunk

Uinta chipmunks were most abundant on rocky slopes (gradient 5), as also reported by Clark and Stromberg (1987). They were relatively more abundant in younger stands (gradient 2). The regression model explained 17% of the variation in abundance of this species (table 4). Compared with the least chipmunk, this species is reported to be more restricted to subalpine forest habitats (Negus and Findley 1959). Telleen (1978) found an association with closed canopy, open understory habitats.

Red Squirrel

Red squirrel abundance was somewhat greater on dry, gently sloping sites (gradients 3, 5), but only 16% of variation in abundance was explained by the regression model. These squirrels were abundant throughout the study area, which seemed to be comprised of excellent red squirrel habitat. Therefore, variation in vegetation among sites was probably minor in relation to the po-

tential variation that would distinguish suitable from unsuitable habitat. Clark and Stromberg (1987) describe red squirrels as widespread throughout coniferous forest habitats of Wyoming.

Deer Mouse

Deer mice were associated with streamside sites having lower basal area of subalpine fir (gradient 3). Although widespread on the study area, they tended to be more abundant on open, lodgepole-dominated sites and meadows than on spruce/fir sites. The regression model explained 15% of the variance in deer mouse abundance (table 4). Contrary to these results, other studies (Brown 1967b, Campbell and Clark 1980, Ramirez and Hornocker 1981) reported associations of deer mice with xeric sites away from streams. The species is known to be abundant on cutover sites (Ramirez and Hornocker 1981, Scrivner and Smith 1984), tolerant of a wide range of ecological conditions (Clark and Stromberg 1987), and omnivorous (Clark 1975).

Southern Red-Backed Vole

This vole, the most abundant species on the study area, was most abundant in mature spruce/fir stands (table 3). Its abundance was also greater in stands that had more herb and grass cover (gradient 1), on northerly slopes (gradient 6), and on sites with greater basal area of subalpine fir and greater log cover (gradient 3). Its abundance was modeled well by the regression, which accounted for 46% of variation in red-backed vole abundance among sites (table 4).

The association of red-backed voles and mature spruce/fir forest is well documented (Ramirez and Hornocker 1981, Allen 1983, Scrivner and Smith 1984). This association may be due, at least in part, to the greater cover of logs and other woody debris that provides protection during critical periods of freezing and thawing (Merritt 1976, 1985; Merritt and Merritt 1978, Sleeper 1979) and supports fungi used as food (Williams 1955, Clark and Stromberg 1987, Wywiowski and Smith 1988).

Western Jumping Mouse

Jumping mice were most abundant in spruce/fir and mature lodgepole habitats (table 3). As reported in other studies (Negus and Findley 1959, Brown 1967b, Clark 1971, Scrivner and Smith 1984), these mice were associated with dense herbaceous or grassy vegetation (gradient 1) along moist streamside (gradient 3) in more mature stands (gradient 2) (table 4). The regression model accounted for 20% of variation in abundance across all stations. These mice feed primarily on grass seeds and fungi (Jones et al. 1978, Vaughan and Weil 1980), which may account for their close association with grassy streamside habitats.

Table 4.—Results of stepwise multiple regressions of small mammal abundance with habitat gradients (principal components from table 2) Sierra Madre, Wyoming.

Species	Habitat gradient ¹						Explained variance ²
	1	2	3	4	5	6	
Masked shrew	(2)	1		4		(3)	0.42
Dusky shrew	(1)	2	(4)			(3)	0.41
Least chipmunk			(1)		2	0.05	
Uinta chipmunk		(2)			1		0.17
Red squirrel		(4)	1	(3)	(2)		0.16
Deer mouse			(1)				0.15
S. red-backed vole	(2)	1	4	5	(6)	(3)	0.46
W. jumping mouse	(1)	2	(3)				0.20

¹Numbers below each gradient indicate the order of entry of that gradient into the stepwise regression (using F-to-enter significance of $P \leq 0.05$). Parentheses indicate negative associations.

²Adjusted R^2 values indicating the proportion of variance in capture (or detection) rates accounted for by gradients included in regression model. All regressions were significant at $P < 0.001$.

General Relationships

Moisture and stand maturity were two habitat features that separated patterns of abundance of the various species. This is illustrated most effectively through the cluster analysis based on interspecific correlations of relative abundance (fig. 2). The dendrogram shows two groups: one comprised of the two shrews, two voles, and jumping mouse; and one comprised of the red squirrel, two chipmunks, and deer mouse. The former group is associated with more moist, old-growth conditions (table 4). The latter group is associated with drier, less mature conditions.

The association of species with old-growth conditions is of special interest because of concern over identifying species that are ecological indicators of old-growth (USDA Forest Service 1985; Nordyke and Buskirk, these proceedings). The Medicine Bow National Forest, the site of this study, lists the southern red-backed vole as an ecological indicator representing late successional stages in conifer forests. Because the forest uses the old-growth scorecard to rate old-growth conditions, whether or not red-backed vole abundance is related to old-growth index values is of interest. Raphael (1987b) confirmed such a trend based on analyses of the first 2 years of the present study.

The trend is even more pronounced when all 3 years are included in the analyses (fig. 3). Southern red-backed voles are increasingly abundant as old-growth scorecard index values increase. Similar trends are evident for masked and dusky shrews (fig. 3).

CONCLUSIONS

The small mammal community, as sampled in this study, was similar in composition to that described in other studies in subalpine forests of the Rocky Mountain region (cf. Ra-

phael 1987a). The southern red-backed vole was the most abundant species and can be considered the species most representative of mature spruce/fir forest stands. Stand age and moisture conditions were the two most important generalized gradients that were predictors of summer abundance of the various species. The southern red-backed vole was confirmed as a suitable ecological indicator of old-growth forest; but, two other species, the masked shrew and the dusky shrew, are good candidates as well.

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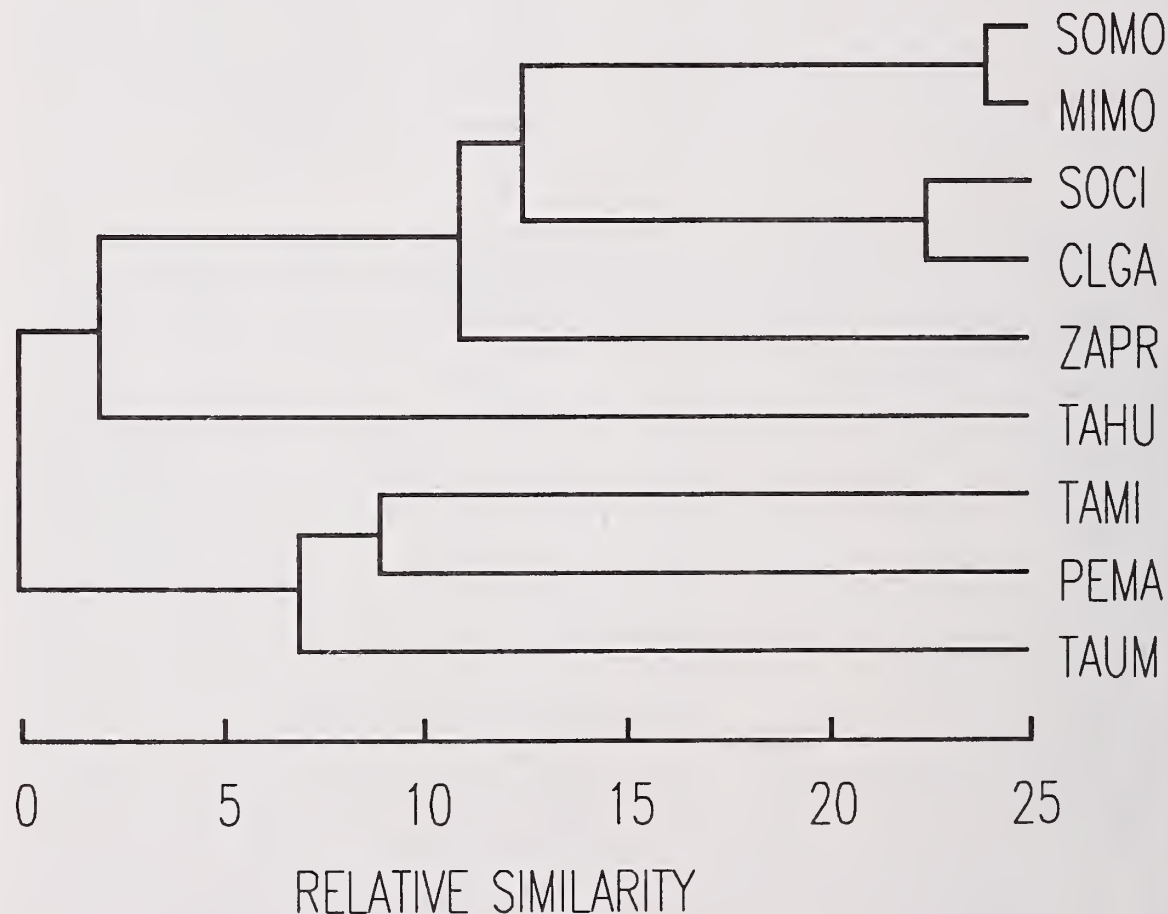


Figure 2.—Dendrogram showing relative similarity (Pearson correlations) of abundances of small mammal species across sampling stations. Species are: *Sorex monticolus* (SOMO), *Microtus montanus* (MIMO), *Sorex cinereus* (SOCI), *Clethrionomys gapperi* (CLGA), *Zapus princeps* (ZAPR), *Tamiasciurus hudsonicus* (TAHU), *Tamias minimus* (TAMI), *Peromyscus maniculatus* (PEMA), and *Tamias umbrinus* (TAUM).

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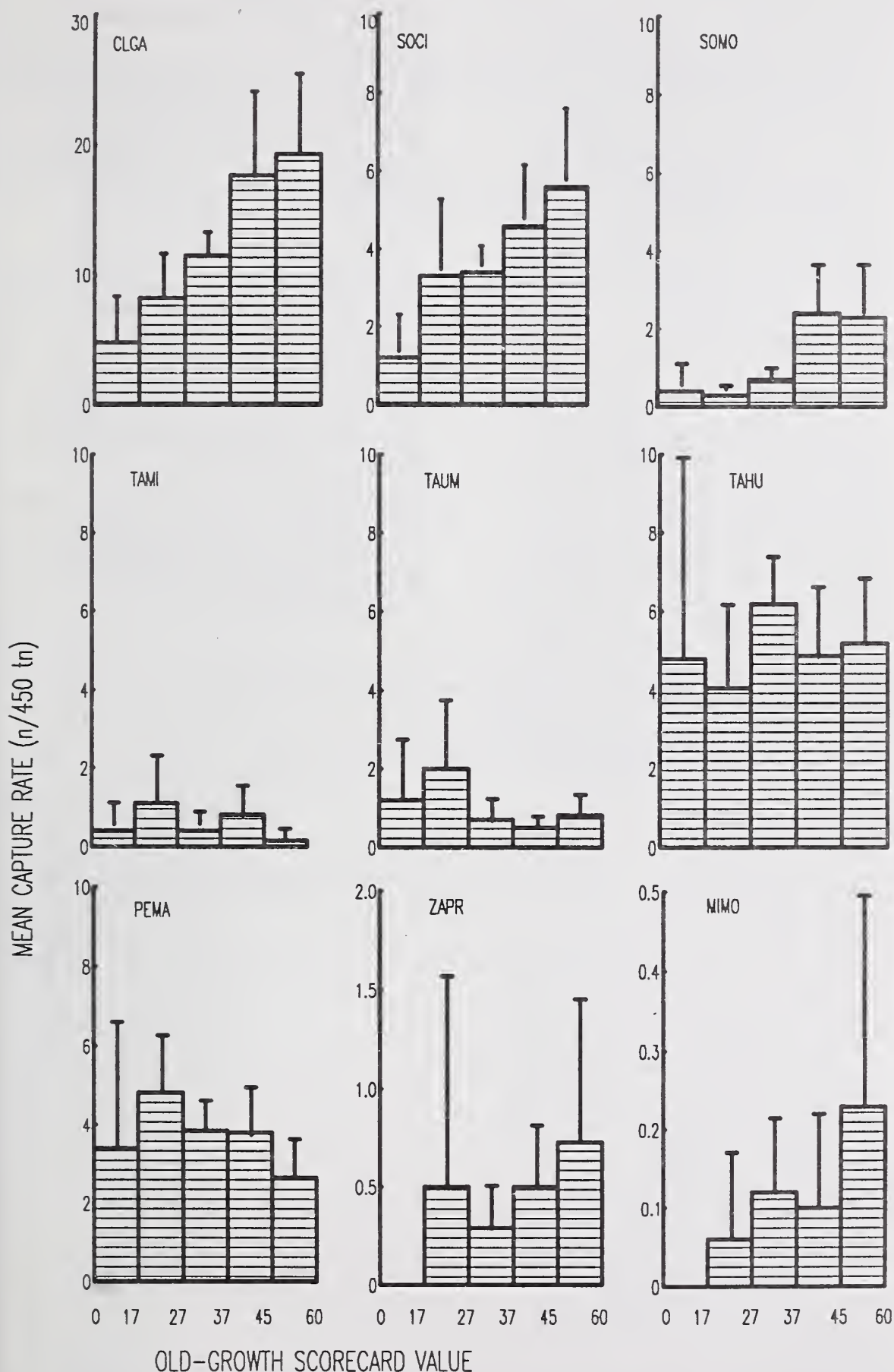


Figure 3.—Mean abundance of selected small mammal species in relation to old-growth scorecard values. Larger scorecard values indicate greater expression of old-growth conditions. Vertical lines within bars indicate 95% CI of means. See figure 3 for species codes.

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Appendix.—Old growth habitat scorecard (Anonymous 1985) used to rate stands in the Rocky Mountain Region. Point values from 1 to 5 are assigned to each category A-L. Values are summed over all rows and the grand total is used as the Index value.

Point value

	5	4	3	2	1
A. Overstory 3 or more species Spruce and/or Fir >50% _____				3 or more species Spruce and/or Fir <50% _____	2 species Spruce and/or Fir >50% _____
					2 species Spruce and/or Fir <50% _____
					1 species 100% _____
B. Midstory 3 or more species Spruce and/or Fir >50% _____				3 or more species Spruce and/or Fir <50% _____	2 species Spruce and/or Fir >50% _____
					2 species Spruce and/or Fir <50% _____
					1 species 100% _____
C. Understory 3 or more species Spruce and/or Fir >50% _____				3 or more species Spruce and/or Fir <50% _____	2 species Spruce and/or Fir >50% _____
					2 species Spruce and/or Fir <50% _____
					1 species 100% _____
D. Total Canopy Cover 70%+ _____				70-50% _____	50-30% _____
					30-10% _____
					<10% _____
E. Overstory, Canopy Cover 50-30% _____				70-50% or 30-10% _____	100-70% or 10-1% _____
F. Midstory Canopy Cover 40-20% _____				70-40% or 20-10% _____	100-70% or 10-1% _____
G. Overstory Ave. DBH (Live) 16"+ _____				15"-13" _____	12"-10" _____
					9"-7" _____
					<7" _____
H. Midstory Ave. DBH (Live) 9"+ _____				8"-6" _____	5"-3" _____
					<3" _____
I. Standing Snags Ave. DBH (Record only those snags above 6' in height.) 16"+ _____				15"-13" _____	12"-10" _____
					9"-7" _____
J. Standing Snags #/Acre (Record only those snags above 6' in height and 7" DBH.) 6+ _____				6-4 _____	3-1 _____
K. Dead, Down Logs Ave. DBH 16"+ _____				15"-13" _____	12"-10" _____
					9"-7" _____
L. Dead, Down Logs #/Acre (Record only those above 7" DBH.) 12+ _____				12-6 _____	6-2 _____
Column Totals	_____	_____	_____	_____	_____

Differences in the Ability of Vegetation Models to Predict Small Mammal Abundance in Different Aged Douglas-Fir Forests¹

Cathy A. Taylor,² C. John Ralph,² and Arlene T. Doyle³

Habitat association patterns have been presented for many small mammal species (e.g. Rosenzweig 1973, M'Closkey 1975, Dueser and Shugart 1978, MacGracken, et al. 1985). In most instances, models representing habitat use have been derived for a single species using a single trapping technique. Most community based studies have also used a single trapping technique. Individual species, however, have different sensitivities to capture, making it difficult to compare capture rates across species (Seber 1981).

To better understand the habitat associations across a sequence of forest ages in the Pacific Northwest, we studied the population status in selected forest stands in northern California and southern Oregon during summer and fall of 1984 and 1985. This study was part of a U.S. Forest Service research project extending from northern California through Oregon and north into Washington (e.g. Ruggiero and Carey 1984, Manuwal and Huff 1987). The impacts of the harvesting of old-growth forests on vertebrate populations in

this area are uncertain (Hagar 1960, Raphael and Barrett 1984, Raphael et al. in press).

We trapped mammals over a gradient of different-aged forest stands using three techniques. Our primary objectives were: (1) to determine if the relative abundance of each species differed between the stands; (2) to determine which habitat variables were associated with the relative abundances of each species; and (3) to study the efficiency of different trapping techniques. In this paper we discuss differences in habitat models derived from different techniques for the five most abundant species of small mammals.

Methods and Materials

Study Area

We selected 47 study stands in three regions of northwestern California and southwestern Oregon. These stands represented a successional gradient typical of the Douglas-fir communities of the region. Stands ranged in elevation from 414 m to 1,556 m and were generally dominated by Douglas-fir in association with tanoak (*Lithocarpus densiflora*) and madrone (*Arbutus menziesii*). Three low elevation stands had a redwood (*Sequoia sempervirens*) component; four high elevation stands in the Cave Junction region were domi-

Abstract.—Three trapping techniques for small mammals were used in 47 study stands in northern California and southern Oregon and resulted in different capture frequencies by the different techniques. In addition, the abundances of mammals derived from the different techniques produced vegetation association models which were often quite different. Only the California red-backed vole (*Clethrionomys californicus*) showed any association with stand age, and no species had any marked associations with the moisture regime of the stands or the geographical region.

nated by white fir (*Abies concolor*).

Fifteen stands were located at each of three regions (in the vicinities of Branscomb and Willow Creek, California, and Cave Junction, Oregon), with an additional 2 stands at Butte Creek, near Dinsmore, California. These stands were divided into three age classes based on core samples of 2 to 10 of the dominant Douglas-firs in each young and mature stand (up to approximately 180 years of age) (B. Bingham, USFS Pacific Southwest Station, pers. commun.). In old-growth stands, tree cores could not always be taken because of large tree size and rotten tree cores, thus some stand ages were based on rings counted on stumps in adjacent clearcuts, along roads, or on core samples provided by local Forest Service offices. Each forest stand was assigned to one of three age classes: young forest < 100 years; mature forest 100-180 years; and old-growth forest, > 180 years. Those that were classified as old-growth forest were further classified as to moisture regime: dry, mesic, or wet, based on species composition and percent cover of the herb and shrub layers of the stand (B. Bingham, pers. commun.). All young and mature stands represented the modal, or mesic moisture class.

An index to the yearly solar radiation was derived by the method of Frank and Lee (1966), which is based on slope, aspect, and latitude. Values are largest on south-facing, moderate

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slopes, and lowest on north-facing, steep slopes.

Mammal Trapping

A single trapping grid for snap/livetrapping was established in each stand in 12 rows, with 12 trap stations per row. Trap stations were placed at 15-meter intervals resulting in a grid 165 m x 165 m. Each stand was relatively homogeneous, and grids located in each stand were, in most cases, separated from different habitat types by at least 100-m of the same habitat.

In 1984, two snaptraps ("Museum Special") were placed in 1984 at each trap station within 1.5 meters of the grid coordinate on all 47 stands. Six stands were trapped simultaneously (two in each region) for five days (four nights) until all stands were sampled (July 3 to August 31). In 1985, a single Sherman livetrapp (7.6 x 8.9 x 22.0 cm) was used at the same stations on 43 of the stands; six stands again were trapped during each five-day session from July 9 to August 30. We did not livetrapp four stands (two in Branscomb area and two in Cave Junction area). In both years, each trap was placed along-

side downed logs, brushy vegetation, or rodent runways. Baited with peanut butter and oat groats in 1984, and oat groats and sunflower seeds (3:1 ratio) in 1985, the traps were left in place for four nights. We feel that the four nights of trapping did not significantly alter populations between years. In the analyses below, we standardized captures to the number per 1000 trap-nights.

We used pitfall traps to sample small mammal populations on all 47 stands during both 1984 and 1985. A pitfall grid consisted of six rows of six pitfall traps per row at 15 m spacing in each stand. Grids were located usually more than 100 m from snap and pitfall grids. Traps were two No. 10 cans taped together and sunk until the top was flush with the ground. A funnel collar to prevent animals from escaping was made from a margarine container with the bottom cut out. We propped a cedar shake 3-4 cm above the opening to the pitfall trap to act as a cover.

Traps were examined at 5-day intervals for 50 days in October and November 1984, and for 30 days in October 1985. In the analyses that follows, we used the number of mammals captured unstandardized for effort.

The complication that not all capture methods were used in both years of the study, resulted in an unknown year-effect that may influence capture frequency. Despite this problem, we feel that the data are instructive as to the variety of models produced, and the implications for investigators.

Vegetation Sampling

Vegetation for each snap/livetrapp grid was measured on 16 plots overlaying the 144 trap stations. Nine vegetation plots were uniformly distributed among the 36 pitfall stations. Vegetation and structure were measured in 5.6 m and 15 m radii circular plots. On each plot, we recorded: percent cover of ground cover variables (i.e. rocks, woody debris); percent cover of vegetation at five height strata; and counts of trees and snags in varying size classes.

We averaged the percent cover values for 25 vegetation stations (16 in the snap/livetrapp grids plus nine stations in the pitfall grids), to obtain mean values of percent cover for 11 ground cover variables and 24 species of plants (or groups of species) in each of the 47 stands (table 1). We combined some taxa into genera prior to calculating means: the true firs (*Abies* spp.), alders (*Alnus* spp.), huckleberries (*Vaccinium* spp.), live oaks (*Quercus* spp.), manzanita (*Artemisia* spp.), various roses (*Rosa* spp.), and *Rubus* spp. The vegetation data were vertically stratified into five levels: ground (0-0.5 m), shrub level (>0.5-2.0 m), mid-canopy (>2.0 m-midlevel), canopy (those trees at the average height of the stand), and supercanopy (those trees substantially above the canopy). Mean values for cover by stand were combined into two strata: "understory" included ground and shrub layers, while "canopy" incorporated mid-canopy, canopy, and supercanopy.

The small and medium trees (<50 cm dbh) were counted on a 5.6 m cir-

Table 1.—Vegetation variables measured for each cluster of trapping stations in a study of small mammal abundance in Douglas-fir forests of southern Oregon and northern California, 1984-85.

Ground cover	Vegetation variables	
Rock	Herb	Dogwood
Soil	Grass	California hazel
Small Litter	Fern	Pines
Moss	Douglas-fir	White and black oaks
Lichen	Tanoak	Salal
First litter layer	Pacific madrone	Manzanita
Second litter layer	Live oaks	<i>Rosa</i> spp.
Solar index	Oregon grape	<i>Rubus</i> spp.
Decay class ^a 1 and 2 logs	Redwood	California laurel
Decay class 3, 4, 5 logs	Poison oak	Huckleberry
	True fir	Big-leaf maples
	Alders	False cedars

^aThomas (1979:80).

cular plot, while large trees (≥ 50 cm dbh) were counted on a 15 m circular plot. The counts of 18 species of trees were averaged over the stations for each grid and were used in an all-subsets regression.

Analyses

We used one-way analysis of variance (ANOVA) to evaluate differences in mammal abundances relative to three stand age classes, three moisture classes of the old-growth stands in each of the three regions (Branscomb and Butte Creek area, Willow Creek area, and Cave Junction area).

These analyses were done on the three separate sets of data, without reference to the each other. Interaction among the factors was ignored in these analyses. When significant differences were found among capture frequencies of individual species by classes of: age, moisture, or study area, a multiple comparison test was used to determine which of the groups were significantly different. A Tukey test (Zar 1984:186) was performed if variances were found to be equal, while a Games and Howell modification was used in the case of unequal variances (Keselman and Rogan 1978).

Pearson product moment correlation coefficients were calculated between capture frequencies for each combination of trapping techniques and between capture frequencies and vegetation means over all stands. Variables from ground cover, herb and shrub cover, and canopy trees were included in all-possible-subsets regression analyses for each small mammal species when a significant correlation existed with capture frequency from any capture technique. Five-variable models were selected for each species when greater than 100 individuals were captured by a particular technique. Vegetation variables were excluded when found on less than 25% of the stands.

Results and Discussion

Twenty-three species of small mammals were captured during the

study, though several were represented by only a few individuals (table 2). The three techniques differed in their effectiveness in captur-

Table 2.—Number of captures by species and trapping technique, from a study of small mammals in northern California and southern Oregon, 1984 and 1985.

Species	Pitfalls	Snaptraps	Livetraps	Total
Trowbridge's Shrew (<i>Sorex trowbridgii</i>)	892	357	101	1350
Pacific Shrew (<i>Sorex pacificus</i>)	33	70	11	114
Vagrant Shrew (<i>Sorex vagrans</i>)	1	1	0	2
Pacific Water Shrew (<i>Sorex bendirii</i>)	1	0	0	1
Shrew-Mole (<i>Neurotrichus gibbsii</i>)	40	27	5	72
Coast Mole (<i>Scapanus orarius</i>)	1	0	0	1
Chipmunks (<i>Tamias</i> spp.)	2	33	282	317
Golden-mantled Ground Squirrel (<i>Spermophilus lateralis</i>)	0	0	1	1
Northern Flying Squirrel (<i>Glaucomys sabrinus</i>)	6	1	8	15
Botta's Pocket Gopher (<i>Thomomys bottae</i>)	5	2	0	7
Deer Mouse (<i>Peromyscus maniculatus</i>)	115	524	404	1043
Pinyon Mouse (<i>Peromyscus truei</i>)	16	205	213	434
Dusky-footed Woodrat (<i>Neotoma fuscipes</i>)	2	4	28	34
Bushy-tailed Woodrat (<i>Neotoma cinerea</i>)	0	0	5	5
California Red-backed Vole (<i>Clethrionomys californicus</i>)	572	161	101	834
Red Tree Vole (<i>Arborimus longicaudus</i>)	1	0	0	1
California Vole (<i>Microtus californicus</i>)	14	14	5	33
Long-tailed Vole (<i>Microtus longicaudus</i>)	2	0	0	2
Creeping Vole (<i>Microtus oregoni</i>)	6	5	10	21
Black Rat (<i>Rattus rattus</i>)	1	0	0	1
Pacific Jumping Mouse (<i>Zapus trinotatus</i>)	3	11	0	14
Short-tailed weasel (<i>Mustela erminea</i>)	0	0	6	6
Number of Trapnights ^a	135,360	55,284	23,367	214,011

^aTotals were adjusted for traps damaged by bears, etc.

ing different species of mammals. Five species had sufficient captures (≥ 100 individuals or more, by one or more of the trapping techniques) to undergo intensive analyses. These were the California red-backed vole, deer mouse, pinyon mouse, Trowbridge's shrew, and the combined chipmunk species.

Associations with Area, Age, and Moisture Class

Most mammals were found in all three areas, with the exception of three species with only 1-2 captured. The California red-backed vole had

significantly fewer captures in the more southerly Branscomb region than in the central and northern regions (table 3). The vole's abundance was significantly correlated with true firs ($r = 0.46$, $P < 0.05$), which were found on 11 stands in the north and no stands in the south. The two mice (*Peromyscus*) species exhibited the opposite trend with captures significantly greater in the south than in the north. The pinyon mouse was correlated with solar index which is generally greater in the southern area. The shrews and chipmunks were found equally in all areas.

The red-backed vole was the only species to have a significant associa-

tion with age of the forest stand ($P < 0.01$). This confirms the study of Raphael and Barrett (1984) and Raphael (this volume) in the Willow Creek area. Our capture frequency was fairly low in stands aged at less than 150 years, while greater densities were evident in many older stands (fig. 1). No such relationship was found for the deer mouse, although Raphael and Barrett (1984) earlier showed a significant association with age in the Willow Creek area.

We tested the abundance of small mammals in the three moisture classes of old-growth forests: dry, mesic, and wet. Among the five mammal species with large sample sizes, there were no differences in capture frequency according to the various moisture classes.

Therefore, we found that within our study areas in the Douglas-fir type, there were few significant or strong associations between five small mammals and age of the forest stand. The stands chosen to represent the different age and moisture classes in this study were all naturally occurring. The young stands originated from fire or other catastrophic events, rather than by timber harvest, and therefore often were heterogeneous in character with structural and floristic components similar to old-growth stands. Scattered old trees and abundant dead and down material were sometimes present in young stands, characteristics which are absent from stands that originated from clearcuts; results in even-aged stands may be very different.

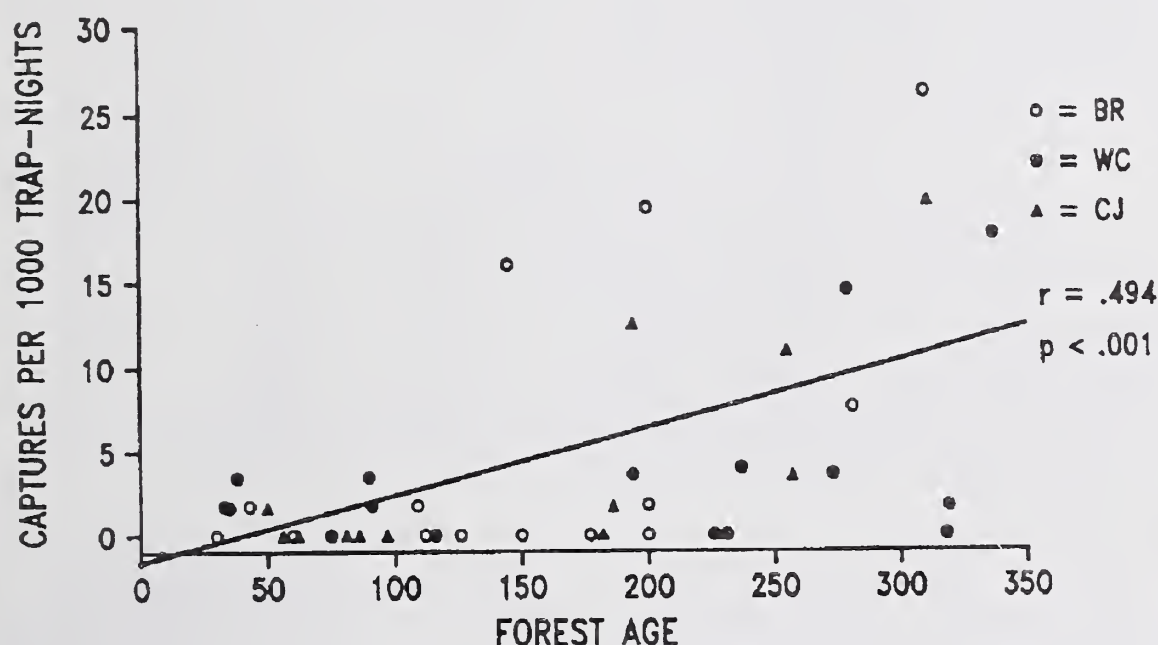


Figure 1.—Captures of California red-backed voles per 1000 trapnights in a study of small mammal abundance relative to stand age, 1984-1985. BR = Branscomb stands, WC = Willow Creek stands, CJ = Cave Junction stands.

Table 3.—Significance of differences in capture frequency by area for five species of small mammals. The areas are CJ = Cave Junction, WC = Willow Creek, and BR = Branscomb and Butte Creek. Methods with no significant differences in capture frequencies at the various areas are indicated by NS; dashed lines indicate inadequate sample size.

Species	Snaptrap	Live trap	Pitfalls
California red-backed vole	NS	NS	BR < WC + CJ
Deer mouse	CJ < WC + BR	CJ < WC + BR	NS
Pinyon mouse	CJ < BR	CJ < BR	—
Trowbridge's shrew	NS	NS	NS
Chipmunks	—	NS	—

Effectiveness of Capture

Captures of small mammals varied greatly by trapping technique (table 1). The two mice were most effectively captured by baited snap and live traps. Very few individuals were collected in unbaited pitfalls. Microtine voles, shrews, and moles were trapped most efficiently by the pitfall

traps and somewhat by snaptraps. Sciurids and woodrats were captured almost exclusively by livetraps.

We correlated the captures of each species by the different techniques. We found significant correlation between capture frequencies only in those techniques effective at sampling large numbers of a particular species (table 4). Demonstrating the closest agreement between techniques were the pinyon mouse ($r = 0.88$ between snap and livetraps) and the vole ($r = 0.73$ between the two years of pitfall traps). The Trowbridge's shrew, on the other hand, showed no relationship between captures by pitfalls and snaptraps ($r = 0.14$), or pitfalls and livetraps ($r = 0.09$). Biological interpretation of such varied results may be very difficult, as discussed in the following.

Vegetation Models

Depending on which method was used to predict the dependent variable, we obtained very different vegetation models, potentially resulting in very different biological interpretations. Models from snap and livetrapping show that areas with high captures of pinyon mice were characterized by high densities of pacific madrone and tanoak, high solar index, and bare soils ($r^2 = 0.64$ and 0.65) (table 5). Four of the five habitat variables were identical in both models suggesting that within our study area, the pinyon mouse used dryer, southern exposures with exposed soils and large amounts of hardwoods.

Models developed for the Trowbridge's shrew from snaptrap and pitfall methods were quite different (table 6). Only one variable was included in both models, and the association with dogwood trees switched from negative to positive. Both models included some indication of greater use of older stands, i.e., the model using snaptrap data included well decayed logs and the livetrapping

model incorporated the decomposed litter layer, representing a well developed layer of organic soil. The inconsistency in these vegetation models was predicted by the lack of correlation between capture frequencies by the two techniques. It appears that in our Douglas-fir habitat type, the shrew may be broadly distributed, independent of finer vegetation composition.

Models for the red-backed vole developed from capture frequencies associated with different trapping techniques (table 7) were more similar than those for the shrew, but less

similar than those for the pinyon mouse. In models developed from snap and livetrapping captures, three of the five variables were selected by both models. Models from pitfall and snaptrap data shared two of the five variables selected. Models from pitfall and livetrapping capture data also shared two of the five variables selected, but one of these variables switched from a positive to a negative association. Only the response to an abundant herbaceous layer was consistent in models from all three trapping techniques. Interpretation of the snaptrap model suggests that

Table 4.—Correlation between years and methods of the capture frequency of four small mammal species in snaptraps (Snap), livetraps (Live), or pitfall traps (Pits). (Chipmunks were only caught in significant numbers in livetraps and could not be compared).

	Between years		Within years	
	Snap84/live85	Pits:84/85	84:pits/snap	85:pits/live
California red-backed vole	0.540**	0.727**	0.459**	0.162
Deer mouse	0.392**	0.015	-0.092	0.320*
Pinyon mouse	0.884**	0.124	0.250	0.320*
Trowbridge's shrew	0.102	0.332*	0.141	0.088

* = $P < 0.05$.

** = $P < 0.01$.

Table 5.—Habitat association models for the pinyon mouse determined from capture frequencies by two different trapping techniques used. NS indicates the variable was not selected, + or - indicates a positive or negative association with capture frequency.

Selected predictor variables	Snaptrap Livetrapping	
Exposed rock	NS	+
Bare soil	+	+
Solar index	+	+
Poison oak	-	NS
Tanoak	+	+
Pacific madrone	+	+
R ²	0.64	0.65

Correlation between capture frequencies of the two techniques = 0.88.

Table 6.—Habitat association models for the Trowbridge's shrew determined from capture frequencies by two different trapping techniques used. Symbols as in table 5.

Selected predictor variables	Snaptrap Livetrapping	
Highly decayed logs	+	NS
Fern	+	NS
Dogwood shrub	+	NS
Dogwood tree	-	+
Deciduous oaks	+	NS
True firs	NS	+
Tanoak	NS	-
California hazel	NS	+
Deep litter layer	NS	+
R ²	0.59	0.55

Correlation between capture frequencies by two techniques = 0.14.

the vole is associated with a fairly moist habitat (abundant herbs and presence of huckleberry). The pitfall model also suggests an association with a moist habitat (more herbs and lichens and less solar index). The livetrapping model includes some indication of moist habitats (herbs, *Rosa* spp., and huckleberry) but also a suggestion of a dryer habitat (solar index).

The deer mouse, despite its abundance, had large differences between variables selected in habitat models (table 8). Its relative abundance did not appear to be associated with the same habitat variables in the same way for the three different trapping techniques. Only two of the 12 variables selected in these models were included in more than one model

with the same sign (avoidance of *Rosa* spp. and preference for areas with California laurel). Model disparity may, of course, simply indicate that one or more of the techniques estimated the dependent variable with considerable bias, thus producing an erroneous model.

The chipmunks were captured primarily by livetrapping. The resulting 5-variable model suggests that chipmunks were more common in the true fir stands at high elevation that had an understory of live oaks and huckleberries (table 9).

While we are sure that there would be some seasonal differences in the habitat association patterns from autumn captures in pitfalls and summer captures in snap and livetraps, we suggest that this seasonal effect would be much less than the differences that we noted, because of the relatively low vagility of the small mammals involved.

All capture methods are assumed to sample individuals of a given species at some unknown proportion of their true abundance. These proportions, within a species, likely differ by capture method. If the capture efficiency of all methods were consistent across sampled areas, then the rank correlation of abundance between methods should be close to 1.0. However, for most species that we studied, correlations of capture frequencies between methods were low and the ranking of stands based

Table 7.—Habitat association models for the California red-backed vole determined from capture frequencies by three different trapping techniques. Symbols as in table 5.

Selected predictor variables	Snaptrap	Livetrapping	Pitfall
Herbs	+	+	+
Rose	-	+	NS
Huckleberry	+	+	NS
False cedar	+	NS	NS
Douglas-fir	+	NS	+
solar index	NS	+	-
Live oaks	NS	-	NS
Lichen	NS	NS	+
Grass	NS	NS	+
R ²	0.58	0.55	0.63

Correlation between capture frequencies: snaptrap and livetrapping = 0.54 ($P < 0.01$); snaptrap and pitfall = 0.50 ($P < 0.01$); pitfall and livetrapping = 0.16 (NS).

Table 8.—Habitat association models for the deer mouse determined from capture frequencies by three different trapping techniques. Symbols as in table 5.

Selected predictor variables	Snaptrap	Livetrapping	Pitfall
Lichen	-	NS	NS
True firs	-	NS	NS
Douglas-fir	-	NS	+
California laurel	+	+	NS
Pacific madrone	-	NS	NS
Manzanita	NS	-	NS
Rose	NS	-	-
Dogwood	NS	+	NS
Deciduous oaks	NS	+	NS
Lower litter layer	NS	NS	+
Herbs	NS	NS	+
False cedars	NS	NS	-
R ²	0.33	0.38	0.63

Correlation between capture frequencies: snaptrap and livetrapping = 0.39 ($P < 0.01$); snaptrap and pitfall = -0.09 (NS); pitfall and livetrapping = 0.32 ($P < 0.05$).

Table 9.—Habitat association models for the chipmunks determined from capture frequencies by livetrapping. Symbols as in table 5.

Selected predictor variables	Livetrapping
True fir	+
Douglas-fir	-
Lichen	+
Vaccinium	+
Live Oaks	+
R ²	0.59

on capture frequencies varied considerably depending on technique used. This suggests that the assumption of a constant proportion of captures, within a given method, across sampled areas was violated.

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Small Mammals in Streamside Management Zones in Pine Plantations¹

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Many second-growth pine-hardwood stands in southern forests are being cut and replaced by pine plantations, especially on industrial land. From 1971 to 1986, the amount of Midsouth timberland in pine plantations increased from 6 to 8% (Birdsey and McWilliams 1986). White-tailed deer adapt well to young brushy clearcuts with ample forage and soft mast. Also, many species of birds are abundant in this diverse brushy habitat (Dickson and Segelquist 1979). But the effects of clearcutting and planting on all vertebrate species are not well assessed or defined.

Various environmental concessions are being implemented along with stand conversion. One practice used to protect water quality and enhance wildlife habitat is to retain mature forest stands along intermittent and permanent streams when adjacent stands are cut and planted to pines (Dickson and Huntley 1986, Seehorn 1986). These areas of mature pine or pine-hardwoods are called riparian zones, filter strips, stringers, streamers, or streamside management zones (SMZ). These areas en-

hance habitat diversity and "edge," offer suitable habitat for wildlife species associated with mature stands, serve as travel corridors for animals, and may permit genetic interchange between otherwise isolated populations of animals. Retention of SMZ for reduction of non-point pollution and for wildlife has been widely recommended.

These mature hardwood strips can be good squirrel habitat. In Mississippi (Warren and Hurst 1980) and in eastern Texas (McElfresh et al. 1980), gray (*Sciurus carolinensis*) and fox (*S. niger*) squirrel numbers were higher in riparian areas than in adjacent upland stands. In another facet of the present investigation, gray and fox squirrels were abundant in SMZ wider than 50 m but virtually absent from zones less than 40 m wide (Dickson and Huntley 1986). A wide variety of reptiles and amphibians were abundant in zones greater than 30 m wide, where a closed canopy offered shaded understory, but were scarce in SMZ less than 25 m wide, which were dominated by low, brushy vegetation (Rudolph and Dickson In Press). The relationships of SMZ and other wildlife species are largely unknown.

The objective of this study was to determine the relationship of SMZ width to small mammal communities. We assessed the effects of narrow (<25 m), medium (30-40 m), and wide (>50 m) SMZ widths on small mammal captures in 6 SMZ in eastern Texas.

Abstract.—Small mammals were captured in live traps in 6 mature-forested streamside management zones of 3 widths, narrow (< 25 m), medium (30-40 m), and wide (50-90 m), which traversed young, brushy pine plantations. More small mammals were captured in the narrow zones (165) than in the medium (82), or wide zones (65).

Study Areas and Methods

Study areas consisted of 6 pine plantations on the western edge of the southern coastal plains in eastern Texas. Mature pine and hardwood trees on the areas had previously been harvested. The plantations had been planted to loblolly pine (*Pinus taeda*) seedlings 5 to 6 years before this study was begun and were vegetated by diverse flora, dominated by hardwood and other woody brush. Oaks (*Quercus* spp.) and sweetgum (*Liquidambar styraciflua*) sprouts, American beautyberry (*Callicarpa americana*), blackberry and dewberry (*Rubus* spp.), and sumac (*Rhus* spp.) were abundant.

Each of the 6 study areas was traversed by a SMZ of mature vegetation. Dominant trees (> 13 cm dbh) in decreasing order of abundance and stem density (No./ha) were as follows: sweetgum, 63; white oak (*Q. alba*), 36; southern red oak (*Q. falcata*), 28; red maple (*Acer rubrum*), 19; black gum (*Nyssa sylvatica*), 14; shortleaf pine (*P. echinata*), 14; and eastern hophornbeam (*Ostrya virginiana*), 14. Dominant understory vegetation (5-13 cm dbh) and stem density (No./ha) included sweetgum, 140; eastern hophornbeam, 71; black gum, 40; flowering dogwood (*Cornus florida*), 40; loblolly pine, 21; and red maple, 19.

Assigned treatments were 3 SMZ widths: narrow (<25 m), medium (30-40 m), and wide (>50 m). Two replications of each treatment were

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sampled at 2 locations. In each of the 6 study areas two 200-m transects were established along each of the 6 streamside zones. Distance from points along the transects to the SMZ edge was variable because each zone orientation changed somewhat with stream meanders. Thirteen Sherman live traps were placed 12.5 m apart on each of the 12 transects. Trapping was conducted 4 consecutive nights in each of 2 consecutive weeks (8 nights) during February and March in 1986 and again in 1987 (52 traps/treatment X 8 nights X 2 years = 832 trap nights). Traps were baited with oatmeal each morning and checked the following morning.

Captures per treatment were approximately normally distributed according to the Kolmogorov-Smirnov Goodness of Fit Test. Each of the 3 treatments was tested for differences between years with the T-Test. There were no significant differences between years ($P > .10$); therefore, capture data were combined for both years. Treatment effects (captures/treatment) were tested for differences by ANOVA and the Duncan's Multiple Range Test at the 0.05 level of confidence.

White-footed mice (*Peromyscus leucopus*) and cotton mice (*P. gossypinus*) were grouped together because of difficulty in positive field identification. Davis (1974) determined that white-footed mouse adults were smaller (15 to 25 g, as opposed to > 30 g for the cotton mouse) and had brighter colors. Also, adult hind-foot length was shorter (21 mm, as opposed to 23 mm for cotton mice). However, numerous sub-adults were captured during the trapping period, making identification extremely difficult.

Results and Discussion

Significantly more small mammals were captured in the narrow SMZ (165) than were captured in the medium (82) or wide (65) SMZ (table 1).

The absence of tree canopy in the narrow zones permitted dense, brushy vegetation growth, abundant seeds, and dense logging slash cover, but medium and wide zones were characterized by shaded sparse understories under closed canopies. Other studies have shown higher densities of small mammals in young brushy stands than in mature stands. In an earlier study in eastern Texas, 64 small mammals were captured in a 6-year-old clearcut, but only 24 in a pine-hardwood stand more than 35 years old. Small mammal species diversity was also higher in the young stand (Fleet and Dickson 1984). In pine plantations in Georgia, small mammal abundance was higher in 1- to 5-year-old pine plantations than in older stands with closed canopies (Atkeson and Johnson 1979). Seed-eaters were abundant in the 1-year-old plantation, but herbivores were abundant in older young brushy stands.

In Pennsylvania, relative abundance of small mammals was greater in recent clearcuts of both northern hardwood and oak forests than in adjacent mature stands (Kirkland 1978). A similar pattern was noted in

deciduous and boreal forests in West Virginia (Kirkland 1977). After clearcutting, small mammal abundance and diversity increased and remained relatively high until stands returned to forest. In Arizona, rodent populations were higher in thinned ponderosa pine (*P. ponderosa*) stands with slash than in unthinned stands (Goodwin and Hungerford 1979).

The most abundant species, the fulvous harvest mouse (*Reithrodontomys fulvescens*) and the white footed mouse/cotton mouse complex, were much more abundant in the narrow zone. For the fulvous harvest mouse, there were 73 captures in the narrow, 4 in the medium, and 3 in the wide zones.

Apparently, the dense brushy vegetation with ample down logging slash provided ideal habitat for this species. There was abundant vegetative forage, seeds, and dense log and brush cover. Schmidly (1983) described the best habitats for fulvous harvest mice in the pineywoods as grassland, pine-grass ecotone, and grass-brush. In an earlier study in eastern Texas (Fleet and Dickson 1984), fulvous harvest mice were captured regularly in a young pine

Table 1.—Number of small mammals captured in streamside management zones in pine plantations (832 trap nights) per treatment.

	SMZ width		
	Narrow	Medium	Wide
Hispid Cotton Rat (<i>Sigmodon hispidus</i>)	9	—	3
Fulvous Harvest Mouse (<i>Reithrodontomys fulvescens</i>)	73	4	3
Eastern Harvest Mouse (<i>Reithrodontomys humulis</i>)	1	—	1
White-footed and Cotton Mouse (<i>Peromyscus leucopus</i> and <i>gossypinus</i>)	76	67	50
Golden Mouse (<i>Peromyscus mottalli</i>)	3	4	—
Florida Wood Rat (<i>Neotoma floridana</i>)	3	5	4
Short-tailed Shrew (<i>Blarina brevicauda</i>)	—	2	4
Totals	165	82	65

plantation, but were not captured in the adjacent mature pine-hardwood stand. In a study of small mammal populations in 5 pine stands in Louisiana, fulvous harvest mice were captured most frequently in a pine seed-tree harvest cut having dense hardwood brush (Hatchell 1964).

Differences among treatments were less pronounced for the *Peromyscus* complex, with captures of 76 in the narrow, 67 in the medium, and 50 in the wide SMZ. In a 1-year-old pine plantation in Georgia, the white-footed mouse was the dominant species (Atkeson and Johnson 1979). It also was the most abundant species in the mature oak-hickory forest type in eastern Tennessee (Dueser and Shugart 1978). Cotton mice were captured regularly in 5 mature pine stands in Louisiana (Hatchell 1964) and in a pine-hardwood stand in eastern Texas (Fleet and Dickson 1984). Neither species was captured in a pine plantation in the Texas study. Schmidly (1983) describes preferred habitat of the cotton mouse as flatland hardwood, flatland hardwood-pine, and lower slope hardwood-pine. McCarley (1954) associated the white-footed mouse with upland forest habitat.

Six other species were not captured frequently enough for conclusions concerning habitat preference. Habitat preferences have been documented to some degree in other studies. The hispid cotton rat is often very abundant and normally is associated with low, dense vegetation (Atkeson and Johnson 1979, Fleet and Dickson 1984, Goertz and Long 1973, Schmidly 1983). It has occasionally been found in habitats dominated by early successional grasses and forbs.

The golden mouse is associated with forested stands having low, dense vegetation (Fleet and Dickson 1984, Hatchell 1964, McCarley 1958). The Florida wood rat occupies forested upland and streamside habitat and thrives in bottomland hardwood stands with low brushy understories (Schmidly 1983). Short-tailed shrews

were captured in the medium (2) and wide zones (4). Other investigations have found them inhabiting a variety of mature stands (Fleet and Dickson 1984, Hatchell 1964, Schmidly 1983).

In conclusion, more small mammals, especially fulvous harvest mice, were captured in narrow SMZ than in medium and wide SMZ. Apparently, this is related to the abundance of low, dense vegetation, with ample forage, fruits, and seeds; and down logs and logging slash. But medium and wide SMZ with closed tree canopies provide limited mature habitat for some species associated with mature stands, such as the short-tailed shrew, and are positive for a variety of other wildlife.

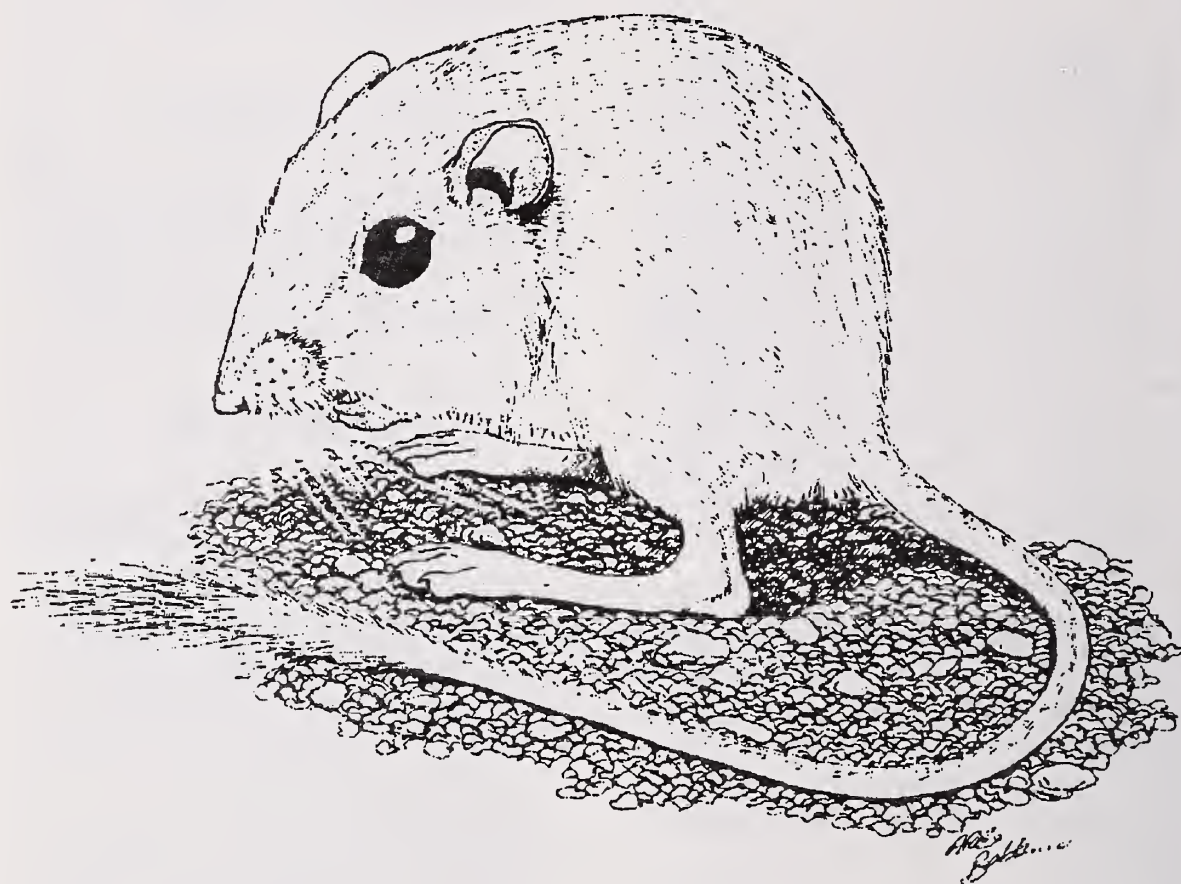
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Patterns of Relative Diversity Within Riparian Small Mammal Communities, Platte River Watershed, Colorado¹

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Riparian communities in the western states are mesic vegetative associations occurring along ephemeral, intermittent, and perennial streams. Although relatively limited in area, these communities contribute more biotic diversity within a region than upland vegetation communities (Thomas et al. 1979).

Riparian communities have been substantially affected by land-use changes such as conversion to agriculture, grazing, and water management (Knopf et al. 1988). Further alterations in the western United States have been caused by the widespread naturalization of salt cedar (*Tamarix* spp.) (Horton 1977) and Russian-olive (*Elaeagnus angustifolia*) (Olson and Knopf 1986). Because of the biological significance and potential for perturbations caused by conflicting land uses, riparian communities have been the focus of numerous technical conferences during the past 10 years (Knopf et al. 1988).

An earlier study of the pattern of avian species diversity in riparian and upland study areas within a watershed (Knopf 1985) showed that

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Abstract.—Relative diversity within and between small mammal assemblages of riparian and upland vegetation was evaluated at 6 study areas across an elevational gradient. In contrast to avian diversity analyses conducted at the same sites, species richness, relative diversity, and faunal similarity of small mammals were greater among upland rather than riparian communities across the cline. Beta diversity between riparian and upland small mammal communities is greater at higher elevations within the watershed. These higher elevation portions of watersheds must be emphasized in management strategies to conserve regional integrity of native small mammal faunas.

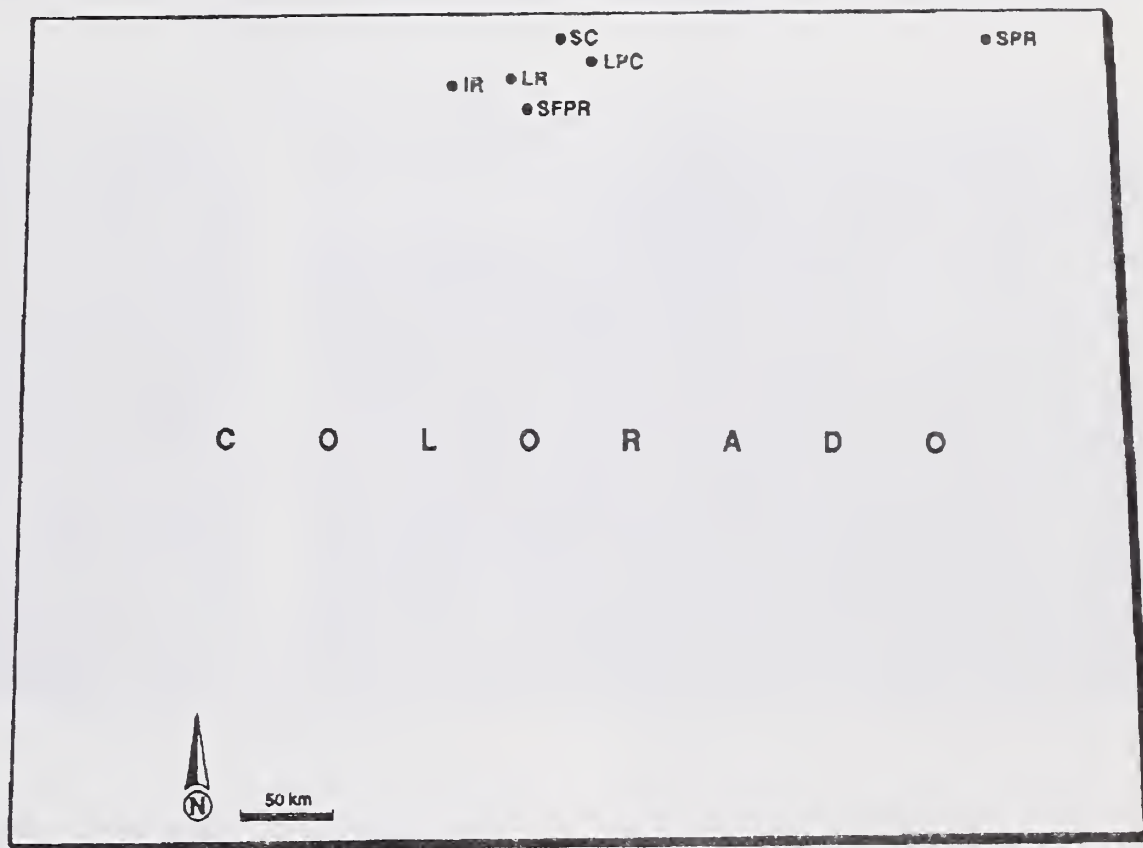


Figure 1.—Location of study areas within the Platte River drainage, northern Colorado, 1981.

although more species of birds occur in riparian vegetation, upland sites contribute more to avifaunal diversity between habitats (beta diversity) and within a region (gamma diversity). Those findings were attributed to greater similarity among riparian avifaunas across the altitudinal cline due to the riparian vegetation providing a corridor for movement of birds within a region. Beta diversity between upland and riparian avian assemblages was greatest at the upper and lower ends of a watershed, and the study concluded that avifau-

nal conservation efforts should be concentrated at those sites.

Implications of the earlier avian study to conservation of small mammal assemblages are unclear. Numerous studies (Anderson et al. 1980; Honeycutt et al. 1981; Kirkland 1981) have examined small mammal distribution along environmental gradients, but with a focus on upland rather than riparian species assemblages. The objectives of this study were to evaluate diversity within, and between, small mammal assemblages of riparian and upland vegeta-



Figure 2.—Study areas: South Platte River (SPR), 1200 m; Lone Pine Creek (LPC), 1909m; Sheep Creek (SC), 2341 m; Illinois River (IR), 2500m; Laramie River (LR), 2631 m; South Fork of the Cache la Poudre River (SFPR), 2747 m.

tion across an elevational gradient. We believed that the results would indicate relative elevations within watersheds at which small mammal conservation efforts should be focused. Such efforts could include policies of state and federal agencies concerning type of land use within portions of watersheds.

Study Areas

Six study areas ranged in elevation from 1200 to 2747 m within the Platte River drainage of northern Colorado (fig. 1). With the exception of an alpine area, riparian communities within each major life zone of upland vegetation along the Front Range were represented (fig. 2). Within each upland, we located a riparian site that contained a permanent stream. Cattle grazing had not occurred on any of the study areas for at least three years prior to 1981.

The South Platte River (SPR) study area was on the South Platte Wildlife Management Area, 2 km south of Crook, Logan County (elevation 1200 m). This community was dominated by sand sagebrush mixed-prairie. Several species of grass and 1 woody species, sand sagebrush (*Artemisia filifolia*), occurred on the upland sandhills. Dominant riparian species were plains cottonwood (*Populus sargentii*), western snowberry (*Symphoricarpos occidentalis*), and willows (*Salix* spp.).

The Lone Pine Creek (LPC) study area was 11 km west of Livermore, Larimer County, at 1909 m elevation. This area of mountain shrub transition vegetation was dominated by true mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), and gooseberry (*Ribes* spp.) in the upland site. The riparian site was dominated by plains cottonwood, willows, and common chokecherry (*Prunus virginiana*). Rocky Mountain junipers (*Juniperus scopulorum*) were scattered throughout both sites.

The Sheep Creek (SC) study areas was 21 km north of Rustic, Larimer County, at an elevation of 2341 m (fig. 2). Ponderosa pine (*Pinus ponderosa*) forest, along with scattered big sagebrush (*Artemisia tridentata*) dominated the upland site. Riparian vegetation was dominated by narrowleaf cottonwood (*Populus angustifolia*), willows, and alders (*Alnus* spp.).

The Illinois River (IR) study area contained sagebrush steppe vegetation and was within the Arapaho National Wildlife Refuge, 10 km south of Walden, Jackson County (elevation 2500 m). Upland vegetation was predominantly big sagebrush. The riparian site included eight species of shrub willows dominated by *S. geyseriana* (Cannon and Knopf 1984).

The Laramie River (LR) study area was 6.5 km north of Chambers Lake, Larimer County (elevation 2631 m). Aspen (*Populus tremuloides*) dominated the upland site, along with Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*). The riparian site was comprised of shrub willows.

The highest study area (elevation 2747 m) was along the South Fork of the Cache la Poudre River (SFPR), at the Pingree Park Campus of Colorado State University, Larimer County. Upland vegetation was composed of lodgepole pine, limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), Douglas-fir, sub-alpine fir (*Abies lasiocarpa*), and a sparse understory of aspen. The riparian site was exclusively shrub willows.

Methods

Small mammal trapping was conducted in 1981 to determine the relative abundances of small mammal species at the 6 study areas. In each study area, two 400-m survey lines were established, including one riparian and one upland site. Riparian survey lines were within riparian vegetation and generally paralleled

the stream course. Upland survey lines began 500 m from the stream and were oriented perpendicular to the direction of the stream.

Trap surveys were conducted between 30 July and 26 August 1981. Survey lines included 20 trap stations spaced 20 m apart. Each trap station contained 1 rat trap and 2 museum special snap traps located within a 1.8-m radius of the measured point. Three traps were used at each station to minimize any bias in the data toward more aggressive species, such as *Peromyscus maniculatus*. Traps were baited with a mixture of ground raisins, carrots, and chipped beef, blended in a peanut butter base, and set for 3 consecutive nights in the riparian and upland sites of a study area simultaneously. Traps were checked in the morning and evening during the 72 hours. Thus, trap effort per study area was 360 trap-nights, including 180 trap-nights each in the upland and riparian sites. Total number of trap-nights for all study areas was 2160.

Diversity indices were calculated to compare species diversity within (alpha) and between (beta) riparian and upland sites across the altitudinal cline. Because preference for type of index varies, we selected two each of the most commonly used indices to measure alpha (Simpson Index, Shannon-Weiner Index) and beta (coefficient of community, percentage similarity) diversity (Whittaker 1975: 95,118).

The former two differ in the general relationship between output value and species diversity. Shannon-Wiener Index (H') varies directly with number of species trapped, while the Simpson Index (C) varies inversely. Coefficient of community (CC) values are ratios of the number of species common to both riparian and upland sites to the total number of species occurring in the two sites combined. Those values are based only on presence or absence and vary directly with diversity. Although percentage similarity values are

based on the differences in importance values between the two sites, they also vary directly with diversity.

Results

A total of 471 small mammals of 22 species was trapped in all study areas in 1981 (table 1). Three species (14% of all species captured) were trapped in riparian sites only, 9 species (41%) were trapped in upland sites only, and 10 species (47%) were trapped in both. Nine species (41%) were rare, being represented by 2 or fewer captures.

Within-Habitat Comparisons

Species composition within riparian sites differed among the study areas. Deer mice (*Peromyscus maniculatus*), voles (*Microtus* spp.), and jumping mice (*Zapus princeps*) accounted for 182 of 189 (96%) total captures at the 3 lower study areas, although jumping mice did not occur at SPR. In contrast, shrews (*Sorex* spp.) accounted for 69% of all captures at the remaining, higher areas. Of 68 small mammals trapped at the higher sites, only 14 (20%) were either voles or jumping mice. No deer mice were trapped in riparian sites at elevations higher than 2293 m.

Changes in species composition of small mammals in upland sites were not distinct. Deer mice were the most frequently trapped of all species at the 4 intermediate study areas. Overall, 112 of 214 (52%) small mammals trapped in the uplands were deer mice. The next 3 species in abundance (least chipmunk [*Tamias minimus*], northern grasshopper mouse, [*Onychomys leucogaster*] and prairie vole [*Microtus ochrogaster*]) accounted for only 67 of 214 (31%) total captures. Of these 4 species, only the deer mouse was trapped at all 6 sites.

Species richness varied among riparian and upland sites. The number of small mammal species trapped in

riparian sites was least at the lowest elevation study area (SPR) and greatest at the second highest study area (LR) (table 2). All other riparian sites were intermediate in species richness with no apparent altitudinal trend. Values for Simpson's Index (C) (a measure of the concentration of dominance) and Shannon-Wiener Index (H') (Whittaker 1975:95) yielded similar results.

The highest diversity among riparian sites occurred at LR, which had the lowest dominance. The SPR study area, which had a high C value, also contained very low species diversity.

The number of small mammal species trapped in upland sites was comparatively high at 2 of 3 study

areas under 2500 m (LPC and SC) and at the highest elevation study area (SFPR) (table 2). Simpson's Index values varied from a high at IR (2500 m elevation) to a low at SFPR (2747 m). Shannon-Wiener values in upland sites ranged from a low of 0.22 at IR to a high of 0.74 at SFPR.

A matrix of percentage similarity values (Whittaker 1975:118) revealed a mean similarity of 0.29 ± 0.06 among upland sites and 0.18 ± 0.05 among riparian sites. These results suggest that small mammal communities in upland sites were more similar across the cline than were those in riparian sites. Overall, beta diversity along the altitudinal gradient was greater (less faunal mixing) in riparian sites.

Table 1.—Species of small mammals trapped at 6 study areas across an altitudinal cline, northern Colorado, 1981.

	Study area ^a											
	SPR		LPC		SC		IR		LR		SFPR	
	Rip ^b	Upl ^c	Rip	Upl	Rip	Upl	Rip	Upl	Rip	Upl	Rip	Upl
<i>Sorex cinereus</i>							8		6		20	3
<i>S. monticolus</i>					1				2		10	1
<i>S. spp.</i>											1	
<i>Sylvilagus nuttallii</i>						1						
<i>Lepus americanus</i>									1			2
<i>Tamias minimus</i>			1	2	15		1	5	17			10
<i>T. quadrivittatus</i>					2							
<i>T. umbrinus</i>					1							2
<i>Spermophilus spilosoma</i>		1										
<i>S. lateralis</i>					2				1			
<i>Thomomys talpoides</i>									1			
<i>Dipodomys ordii</i>		4										
<i>Reithrodontomys megalotis</i>	2	2	1	1								
<i>Peromyscus maniculatus</i>	65	1	42	68	7	16		18		3		6
<i>Onychomys leucogaster</i>		10						2				
<i>Neotoma mexicana</i>			1									
<i>Clethrionomys gapperi</i>												8
<i>Microtus longicaudus</i>					1	6						
<i>M. ochrogaster</i>			33	11								
<i>M. spp.</i>			2	1			8		1			
<i>Lagurus curtatus</i>				1								
<i>Zapus princeps</i>			4		23	1	1		4			
Totals	67	18	83	84	39	38	17	21	20	21	31	32

^aStudy areas: SPR = South Platte River; LPC = Lone Pine Creek; SC = Sheep Creek; IR = Illinois River; LR = Laramie River; SFPR = South Fork of Cache la Poudre River.

^bRip = Riparian site.

^cUpl = Upland site.

Between-Habitat Comparisons

Species richness was substantially higher in upland sites than in adjacent riparian sites at the lowest and highest study areas (table 2). The values were similar at 3 study areas of intermediate elevation. Only at LR (the second-highest area) was species richness higher in the riparian site. At that study area, number of species trapped in riparian was greater than the upland even when captures of

Lepus americanus and *Thomomys talpoides* were excluded.

Coefficient of community (CC) values (Whittaker 1975:118) suggest that small mammal communities in riparian and adjacent upland sites were relatively similar at lower elevations, and became more dissimilar at 2500 m and higher (table 3). More species (3) were common to both riparian and upland sites at the 3 lower study areas than at the higher areas. Percentage similarity (PS) val-

ues indicate the same trend, with the exception of the lowest study area. The low value at that study area is due primarily to the abundance of *Peromyscus maniculatus* dominating this calculation (table 1).

Discussion

To date, studies of small mammal distribution along environmental gradients (Anderson et al. 1980; Armstrong et al. 1973; Honeycutt et al. 1981; Kirkland 1981) have been conducted in upland sites. Knopf (1985) compared distribution of breeding birds in riparian and adjacent upland sites within the 6 areas used in this study. The focus of this study was to analyze patterns of small mammal faunal similarity within and between riparian and adjacent upland sites in the same watershed. Such patterns, although based on relatively small sample sizes, may indicate elevations along the gradient at which management should be emphasized to conserve regional diversity.

A pronounced change in species composition occurred within riparian sites at 2500 m elevation. The study areas below that elevation, representing foothills and plains, were dominated by deer mice and voles. At 2500 m and above, dominance shifted primarily to shrews. The means for PS values comparing the 3 lower study areas (0.31 ± 0.10) and 3 higher study areas (0.43 ± 0.02) were both considerably higher than the mean for all study areas (0.18 ± 0.05). Faunal similarity changed as riparian sites shifted from cottonwood-willow to willow shrub systems. This shift in small mammal community composition could have reflected a shift from xeric site willows (*S. amygdaloides*, *S. exigua*) to mesic site willows as described in Cannon and Knopf (1984). Other factors may have influenced composition of small mammal communities. Among those suggested in previous research are

Table 2.—Species richness (Simpson Index = C) and relative alpha diversity (Shannon-Wiener Index = H') of small mammals across an altitudinal cline, northern Colorado, 1981.

Study Area	Riparian			Upland		
	Number of species	(C) ^a	(H') ^b	Number of species	(C)	(H')
South Platte River (SPR)	2	0.94	0.06	5	0.38	0.53
Lone Pine Creek (LPC)	6	0.42	0.46	7	0.67	0.30
Sheep Creek (SC)	5	0.40	0.50	7	0.34	0.58
Illinois River (IR)	3	0.45	0.38	3	0.75	0.22
Laramie River (LR)	7	0.21	0.74	3	0.68	0.26
South Fork of Cache la Poudre River (SFPR)	3	0.52	0.33	7	0.21	0.74

$$^aC = \frac{\sum_{i=1}^s p_i^2}{\sum_{i=1}^s p_i} = \frac{\sum_{i=1}^s (n_i/N)^2}{\sum_{i=1}^s (n_i/N)}$$

$$^bH' = -\sum_{i=1}^s p_i \log p_i$$

Table 3.—Between habitat (beta) diversity of small mammal communities in riparian and adjacent upland sites at 6 areas across an altitudinal cline, northern Colorado, 1981.

Study area	No. species (riparian/upland)	Species common to both sites	(CC) ^a	(PS) ^b
South Platte River (SPR)	2/5	2	0.57	0.08
Lone Pine Creek (LPC)	6/7	4	0.62	0.66
Sheep Creek (SC)	5/7	3	0.50	0.26
Illinois River (IR)	3/3	0	0.00	0.00
Laramie River (LR)	7/3	1	0.20	0.25
South Fork of Cache la Poudre River (SFPR)	3/7	2	0.40	0.12

$$^aCC \text{ (Coefficient of community)} = 2S_{\alpha\alpha}/(S_a + S_b)$$

$$^bPS \text{ (Percentage similarity)} = \min(p_a \text{ or } p_b)$$

soil type, nutrient availability, and vegetation structure (Huntley and Inouye 1984, Moulton et al. 1981). Others have found specific microhabitat components to be important (cf. M'Closkey 1981, Szaro and Belfit 1987).

Dominance by deer mice was particularly obvious at the lowest site, SPR, where 65 of 67 captures were of this species. The remaining 2 small mammals trapped were western harvest mice (*Reithrodontomys megalotis*). These findings were supported by an earlier study of total small mammal richness conducted in the same study area. During the 1982 and 1983 field seasons of that study, 98.3% of all small mammals captured in 25,000 trap-nights were deer mice and western harvest mice (Bennett 1984).

High numbers of deer mice trapped could indicate behavioral differences (deer mice being more aggressive), rather than a dominance in absolute numbers. We believe, however, that the number trapped reflected higher relative abundances of *Peromyscus maniculatus* for several reasons. First, although this species was the most frequently trapped species, it dominated only 4 of 12 total sites, and was infrequent to absent at 7 sites (table 1). Total captures in 180 trap-nights at each of those 4 sites (riparian at SPR, upland at IR, both sites at LPC), ranged from 18 to 68. That is, deer mice captures accounted for no more than 38 percent of all available traps at any site. Moreover, in the riparian site at SPR (where deer mice were most commonly caught), the percentages of all captures that were deer mice were similar for this study (97%) and that of Bennett (1984) (95%).

Dominance by ecological generalists at the lowest site, SPR, likely is explained by periodic catastrophic events, specifically flooding. In contrast to periodic severe flooding observed in floodplains of the western Great Plains, riparian systems at higher elevations are not subject to severe overbank flooding. During a

study of riparian avifauna at SPR, annual spring flooding varied tremendously (Knopf and Sedgwick 1988). Maximum mean daily flow in 1982 was 44 m³/sec, compared to 405 m³/sec in 1983, when all of the riparian zone, as well as portions of adjacent upland habitat were flooded. No overbank flooding occurred in 1982. Habitats of small mammals in lower riparian systems are periodically subjected to total inundation for variable amounts of time. Those habitats appear to be too unstable to assure prolonged survival by species populations, and are recolonized by individuals from the uplands following each perturbation.

Changes in small mammal communities among upland sites were less pronounced. Faunal similarity was greatest at the intermediate sites, especially LPC (1909 m), SC (2293 m) and IR (2500 m). The mean of PS values comparing those sites was 0.57 ± 0.12 , compared to the overall mean of 0.29 ± 0.06 . Deer mice were a dominant species at all sites but SPR (sand sagebrush mixed-prairie) and LR (aspen). The distribution of other species appeared to be influenced by changes in upland vegetation types along the altitudinal gradient. For example, northern grasshopper mice were relatively abundant at the lowest site, which contained grassland areas. Boreal redback voles (*Clethrionomys gapperi*) were similarly abundant at the highest site in spruce-fir. Neither species was trapped elsewhere. Honeycutt et al. (1981) also reported that the distribution of some species along an altitudinal gradient in Utah was strongly influenced by type of vegetation. We (Knopf and Olson 1984) have noticed regional differences in small mammal communities in riparian zones of similar woody communities but different herbaceous composition that can be attributed to variations in site dryness.

Beta diversity was low (high CC values) at elevations of less than 2500 m (SPR, LPC, and SC), indicating

that small mammal communities in riparian and adjacent upland sites were quite similar. At 2500 m (IR), the CC value declined to 0 (no species common to both sites), then remained low at the higher study areas that contained aspen and spruce-fir uplands. With the exception of an extremely low value at SPR (caused by the overwhelming dominance of deer mice in the riparian site), PS values followed the same pattern. Thus, within the Platte River watershed, beta diversity between riparian and upland small mammal communities is much greater at the upper end of the altitudinal cline.

These results differ from the avifaunal studies of Knopf (1985) who found beta diversity between riparian and upland sites to be greatest at the higher and lower ends of the watershed, and upland/riparian assemblages to be similar at intermediate study areas. Also in contrast to Knopf's (1985) findings were greater relative diversity in, and faunal similarity among, upland communities. In support of the avian study conclusions, however, riparian sites at the higher elevations contributed substantially to small mammal beta and gamma (regional) diversity.

Implications to Conservation

Historically, management of riparian zones has occurred primarily on areas at lower elevations. Management that is concentrated in a limited number of habitats or at selected elevations may result in higher local (alpha) diversity at the expense of beta and gamma (regional) diversity (Samson and Knopf 1982). Despite different beta diversity patterns, our findings support the conclusion by Knopf (1985) that greater emphasis needs to be placed upon conservation of riparian communities at higher elevations regionally.

Knopf et al. (1988) have recommended that agencies develop guidelines for regionwide rather than local

management of riparian systems. Respective agencies should realize that small mammal communities at higher elevations contribute more to regional diversity than those at lower elevations. In order to conserve regional integrity in native small mammal faunas, land uses allowed in, and adjacent to, high elevation riparian zones should be critiqued as carefully as those in lowland floodplains. For example, livestock grazing can affect structure of small mammal associations by reducing understory vegetation (Moulton et al. 1981). Grazing and other activities that potentially reduce understory vegetation in higher elevation riparian zones can seriously affect abundances of certain species such as shrews that are not present at lower sites. The consequences to regional diversity of small mammals would be greater than livestock grazing at lower elevations because our findings suggest that: (1) higher elevation (above 2500 m) sites contribute more to regional diversity of small mammals; and (2) small mammal communities in some lower elevation riparian zones are composed mostly of species populations of ecological generalists that are regulated by catastrophic, natural perturbations.

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Estimated Carrying Capacity for Cattle Competing with Prairie Dogs and Forage Utilization in Western South Dakota¹

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On the Great Plains, black-tailed prairie dogs (*Cynomys ludovicianus*) compete with livestock for forage and have been a major concern among livestock producers since the late 1800's (Merriam 1902). For livestock producers, increased cattle-carrying capacity on range land is the primary objective of large-scale prairie dog control programs (Collins et al. 1984). However, carrying capacities for cattle have not been fully evaluated comparing effects in the presence versus the absence of prairie dogs. Carrying capacities for cattle competing with prairie dogs for forage have historically been determined by estimating standing crop of herbage and then arriving at range condition and estimated carrying capacity. Information on diets of cattle and prairie dogs, consumption rates, production of forage, and prairie dog densities has never been collectively evaluated to determine carrying capacities on rangelands supporting both cattle and prairie dogs.

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Abstract.—Carrying capacities for cattle competing with black-tailed prairie dogs (*Cynomys ludovicianus*) were estimated by a linear programming technique for management of cool-season grasses in western South Dakota. Forage utilization was allowed to range from 20% to 80%. Under management for cool-season grasses (western wheatgrass (*Agropyron smithii*); needlegrasses (*Stipa* spp.)), stocking rates of cows ranged from 43 to 214 per hectare over a 6-month grazing season, and cow-calf stocking rates ranged from 43 to 214 per hectare over a 6-month grazing season, and cow-calf stocking rates ranged from 23 to 161. Needlegrasses and needleleaf sedge (*Carex eleocharis*) were key forage species.

This study utilized a linear programming approach (GOAL) to determine carrying capacities of cattle as limited by prairie dog town sizes and forage utilization while still maintaining pastures in a near climax stage of mixed perennial cool-season grasses. Cool-season grasses included western wheatgrass (*Agropyron smithii*) and needlegrasses (*Stipa* spp.).

Study Area and Methods

The study was conducted in Conata Basin, approximately 29 km south of Wall, S. Dak. Average annual precipitation at the Cedar Pass Visitor Center, Badlands National Park, approximately 21 km east of the study area, is 39.7 cm, of which 79% falls from April through September. Average annual temperature is 10°C. Effective forage-year (October 1 to September 30) precipitation for plant growth was 46.3 cm.

Major graminoids of the study area included blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), western wheatgrass, needleleaf sedge (*Carex eleocharis*), and red threeawn (*Aristida longiseta*). Common forbs were scarlet globemallow (*Sphaeralcea coccinea*), Patagonia Indianwheat (*Plantago patagonica*), and prairie dogweed (*Dysodia papposa*). Shrubs were snakeweed (*Xanthocephalum sarothrae*) and silver sagebrush (*Artemisia cana*).

The area is grazed by cattle and black-tailed prairie dogs. Prairie dogs graze within towns and were active throughout most of the year. Cattle grazed the entire area from approximately mid-May to the last of October. Stocking levels of cattle varied from year to year depending upon moisture levels and available forage.

We applied the GOAL computer program to a resource decision problem using data from a 2,100-ha pasture following similar procedures by Bartlett et al. (1976), Bottoms and Bartlett (1975), and Connolly (1974). Basic data collected on or near the pasture included cattle diet composition (Uresk 1986), black-tailed prairie dog diet composition (Uresk 1984), prairie dog densities (Cincotta 1985), and forage production (Uresk 1985). Forage consumption of a cow and cow-calf unit was estimated as 355 kg/month [1 AUM (Animal Unit Month)], and 485 kg/month (1.32 AUM), respectively (USDA 1968). Forage consumption of a black-tailed prairie dog over a 12-month period was estimated at 10.95 kg (Hansen and Cavender 1973). Prairie dog densities were estimated as 44 animals/ha (Cincotta 1985).

Seral stages (table 1) were estimated for the entire pasture, based on discriminant functions developed for canopy cover and frequency of occurrence of major plants. Climax or near-climax (seral stage A) was dominated by western wheatgrass; seral stage B was high in blue grama;

while seral stage C was high in buffalograss. Range seral stage D consisted of approximately equal but smaller amounts of all three plant species. Estimates of forage production and area occupied by prairie dog towns were specified separately for each range seral stage in the analysis.

In the analysis, forage utilization was varied for the entire pasture at four levels (20%, 40%, 60% and 80%) when both cattle and prairie dogs were grazing. Prairie dog towns were allocated to seral stages B, C, and D; but not to range condition class A because prairie dogs do not occur in or near climax vegetation. Prairie dogs were confined to areas that totalled from 20 to 40 ha for the entire pasture. Forage utilization on these areas was adjusted to 100%.

Major forage plants of both herbivores included western wheatgrass blue grama, buffalograss, needleleaf sedge, sand dropseed (*Sporobolus cryptandrus*), needlegrasses, scarlet globemallow and categories of other graminoids, and other forbs (Uresk 1984, Uresk 1986). Shrubs were excluded because they were minor components of the diets and rangeland. Average herbivore diets for the season were used in this linear programming analysis.

With linear programming, management options for amounts of forage utilization and area occupied by prairie dog towns were analyzed under management for cool-season grasses. Under management for cool-season grasses, no forage species was utilized over the selected percentages.

For the GOAL programming analysis, the following assumptions were made:

1. Adequate forage of major plant species were available within limits of prescribed utilization so that herbivores did not adjust their normal diets and consumption in response to a decrease in forage.

2. Common use of the range by the two herbivores did not alter the preference for forage within established utilization limits.

3. Forage consumption was proportional to population densities of the herbivore species.

Cattle stocking numbers were estimated as follows. Diet composition and forage consumption rates of both herbivores were specified and held constant. Forage availability was specified for each species by seral stage and held constant. Prairie dog density per hectare of town was specified and held constant. The management variables—percent forage utilization and hectares in dog towns—were varied within specified limits.

Finally, the GOAL program solved cattle-stocking numbers that could be supported by the available forage for a given forage utilization percentage and hectares in prairie dog towns. When present, prairie dogs were given first priority for forage.

Results

Plant Production

Forage production for individual species was greatest for western wheatgrass, followed by buffalograss and blue grama (table 1). The pasture at or near climax seral stage (A) had the lowest plant production (1970 kg/ha); seral stage C had the greatest overall production (2267 kg/ha). Most of the pasture was at or near climax seral stage A (58%) and did not have prairie dogs, a factor that results in a relatively low impact by prairie dogs. Seral stages B, C, and D made up 3%, 7%, and 32%, respectively, of the pasture. All had prairie dogs residing.

Carrying Capacity

Carrying capacity for mature cows without calves (6-month grazing period) on range with no prairie dogs competing ranged from 55 to 221 cows/2100 ha when forage utilization levels were from 20% to 80%

Table 1.—Estimated peak plant production (kg/ha) (Uresk 1985) by range class on a 2,100-ha pasture.

Plant taxa	Range seral stages ¹ (ha)			
	A (1226)	B (55)	C (144)	D (675)
Western wheatgrass (<i>Agropyron smithii</i>)	1354	514	72	301
Blue grama (<i>Bouteloua gracilis</i>)	204	441	396	88
Buffalograss (<i>Buchloe dactyloides</i>)	47	601	1172	192
Needleleaf sedge (<i>Carex eleocharis</i>)	9	12	43	38
Needlegrasses (<i>Stipa</i> spp.)	32	44	0	55
Sand dropseed (<i>Sporobolus cryptandrus</i>)	0	1	5	48
Other graminoids	138	180	253	372
Total graminoids	1784	1793	1941	1094
Scarlet globemallow (<i>Sphaeralcea coccinea</i>)	36	36	47	96
Total forbs	150	388	279	1046
Total production ²	1970	2217	2267	2236

¹A = climax; D = low seral stage. Uresk, D. W. submitted. A quantitative method for estimating ecological stages in a mixed-grass prairie with multivariate techniques. J. Range Manage.

²Shrubs are not included in production estimates.

(table 2). In estimating stocking rates, no single forage species was allowed to be utilized at levels greater than the set levels from 20% to 80%. Thus, a range of 1.6 to 6.4 ha/AUM was required. Numbers of cows decreased as hectares of prairie dog towns increased; stocking rates decreased by approximately 3 for every additional 20 ha of prairie dogs (880 prairie dogs or 293 prairie dogs/cow) up to 40 ha on the pasture.

Cow-calf stocking rates ranged from 40/2,100 ha to 161 (1 cow-calf unit = 7.92 AUMs for 6-months) when utilization levels varied from 20% to 80% without prairie dogs (table 2). At these stocking rates, approximately 2.1 to 8.7 ha were required for each AUM. Stocking rates decreased by approximately 2 cow-calf units for every additional 20 ha of prairie dogs.

Discussion

Needlegrasses and needleleaf sedge limited carrying capacity for cattle on pastures managed for cool-season grasses. Western wheatgrass was never a limiting species; that is, consumption of western wheatgrass by both herbivores never exceeded the amount available. The 80% level of

utilization of some cool-season grasses is too high to maintain the viability of these plants, and lower utilization levels (30-45%) are recommended (Lewis et al. 1956). With fewer cattle grazing under management for cool-season grasses, cattle gain more weight per day, but fewer kilograms per hectare (Black et al. 1937, Lewis et al. 1956, Bement 1969).

Prairie dog expansion can be reduced under management for cool-season grasses because vertical cover and grass heights increase (Cincotta 1985). Prairie dogs did not significantly expand over a 4-year period on areas where cattle were excluded (Uresk et al. 1982). Furthermore, a lower stocking rate (management for cool-season grasses) would increase vertical grass cover on the range and would thereby further reduce prairie dog expansion. Snell and Hlavachick (1980) and Snell (1985) reported reduced expansion rates and elimination of prairie dog colonies by using a summer-deferred grazing system. Prairie dogs prefer habitat managed for warm-season grasses [blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*)]. Increased stocking rates of cattle and shortgrass stature with low vertical cover allows for prairie dog expansion (Uresk et al. 1982, Cincotta 1985).

Cattle stocking rates estimated in this study were conservative, because upper limits of forage consumption and prairie dog densities (44 animals/ha) were used in the analyses. The guidelines reported here for cow or cow-calf stocking rates for cool-season grasses represent viable options for management. Key forage species used to estimate cattle numbers and monitor utilization for management of cool-season grasses included needlegrasses and needleleaf sedge. Generally, stocking rates were limited by production and use of needlegrasses, although needleleaf sedge and sand dropseed also influenced cow numbers. When hectares of prairie dogs are high, needleleaf sedge can become the major limiting factor in determining cow numbers. Needlegrasses were generally the limiting plant component in determining cow-calf units. Sand dropseed can be limiting when the area with prairie dogs is greater than or equal to 200 ha.

This study only presents estimates for up to 40 ha of prairie dog colonies (approximate current levels of prairie dogs) on a 2,100-ha pasture, and limited extrapolation is suggested beyond data in table 2. An additional constraint is availability of needlegrasses and needleleaf sedge. Extrapolation of results to pastures with lower availability of these species should be done cautiously. In fact, where forage availability and composition are much different from the pasture studies, extreme care should be used in extrapolating results to other areas. The assumptions and required constraints for GOAL linear program analysis imposes some limitations on biological sensitivity.

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Table 2.—Estimated 6-month carrying capacity for mature cows with and without calves with management for cool-season grasses. Stocking rates are related to hectares of prairie dogs and allowable forage utilization on a 2,100-ha pasture in western South Dakota. Consumption of needlegrasses and needleleaf sedge is 100% on prairie dog occupied areas.

Forage utilization %	Prairie dogs occupied areas (ha)					
	0	20	40	0	20	40
	Cow numbers ¹			Cow-calf numbers ²		
20	55	53	50	40	39	37
40	110	108	105	81	79	77
60	166	163	160	121	119	117
80	221	218	214	161	159	157

¹355 kg of forage consumed/cow/month (1 AUM).

²485 kg of forage consumed/cow-calf/month (1.32 AUM).

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Cattle Grazing and Small Mammals on the Sheldon National Wildlife Refuge, Nevada¹

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Abstract.—We studied effects of cattle grazing on small mammal microhabitat and abundance in northwestern Nevada. Abundance, diversity, and microhabitat were compared between a 375-ha cattle exclosure and a deferred-rotation grazing allotment which had a three-year history of light to moderate use. No consistent differences were found in abundance, diversity, or microhabitat between the two areas.

Grazing by livestock is a common and economically important practice throughout much of the western United States. Because grazing alters wildlife habitat, much attention has centered on its impact on wildlife abundance, diversity, and habitat use. However, relatively little information exists on effects of grazing on small mammal communities. Such information would aid development of effective grazing programs where small mammals are a management concern.

Several authors have demonstrated that removal or alteration of cover can cause changes in small mammal communities (Birney et al. 1976, Geier and Best 1980, Grant et al. 1982, LoBue and Darnell 1959). More specifically, grazing altered rodent species diversity through changes in plant species diversity on several habitats in northeastern California (Hanley and Page 1982). Similarly, Grant et al. (1982) found differential changes in several small mammal community parameters between

grazed and ungrazed sites in four western grassland communities; tall-grass and montane grasslands appeared to be most affected by grazing.

In assessing grazing impacts on small mammal communities, Hanley and Page (1982) stressed the importance of evaluating effects on a habitat-type basis. Grant et al. (1982) concluded that the response of a small mammal community to grazing depended on the site and the original mammal species composition.

In 1980, the Sheldon National Wildlife Refuge (SNWR) initiated a deferred-rotation grazing system on the 6,954-ha Badger Mountain grazing allotment to improve soil and range conditions. The management plan was designed to graze 1,444 animal-unit-months (AUMs) with the grazing period alternating between mid-June through early August during one year and early August through late October the next (five-year average, David Franzen, Range Conservationist, SNWR, pers. comm.). Prior to 1979, the allotment had been on a season-long grazing system from early April through September with an estimated 1,700 AUMs being removed from the unit (U.S. Fish and Wildlife Service 1980).

In Spring 1981, we constructed a 375-ha cattle exclosure on the Badger Mountain allotment to evaluate the effects of cattle grazing on wildlife and their habitat (Oldemeyer et al. 1983). The purpose of this element of

the study was to evaluate the effect of the grazing system on small mammals. Specifically, we wanted to determine the following: (1) is there a difference in small mammal abundance and diversity between the areas over time, (2) is there a difference in the available small mammal habitat between areas, and (3) what microhabitat characteristics are indicative of capture sites by individual small mammal species for the two ecosites? We tested the null hypothesis of no significant difference between the exclosure and the allotment.

Study Area and Methods

The Badger Mountain allotment ranges from 1,890–2,152 m elevation and is composed of two dominant range ecosites (Anderson 1978). The shrubby rolling hills (SRH) ecosite occurs on moderate to deep soils and is dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*) with grass understory dominated by Idaho fescue (*Festuca idahoensis*). The mahogany rockland (MR) ecosite occurs on rocky ridges and slopes with bedrock outcrops. Curlleaf mountain mahogany (*Cercocarpus ledifolius*) is predominate in this ecosite with a grass understory dominated by western needlegrass (*Stipa occidentalis*) (fig. 1). Precipitation on Badger Mountain ranges from 27–33 cm an-

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nually with most coming as snow and as spring and autumn rains (U.S. Fish and Wildlife Service 1980).

We conducted the study during the summers of 1983 and 1984, four and five years, respectively, after initiation of the deferred-rotation grazing system. Grazing intensities were 1,650 AUMs from 10 July to 10 August, 1980, 1,770 AUMs from 7 August to 30 September, 1981, and 1,036 AUMs from 24 June to 22 August, 1982. In 1983, cattle were grazed on the allotment from 1 August through 15 October at a rate of 980 AUMs. The following year, the unit supported 1,337 AUMs during a 28 June to 18 August grazing period (David Franzen, Range Conservationist, SNWR, pers. comm.).

In 1983, eight live trap grids were established with trap stations 15 m apart. Four grids were located inside the enclosure and four were located in the allotment. We arranged each 7 X 7 grid so that approximately half of the traps were in the SRH ecosite and half were in the MR ecosite. We sampled only four grids (two in the enclosure and two in the allotment) in 1984, but we increased the size of the grids to 64 (8 X 8) trap stations.

We trapped from 1 July through 11 August in 1983, and 19 June through 1 July in 1984. Only one pair of grids were trapped at a time (one grid in the enclosure, one in the allotment), for a total of four trap sessions in 1983, and two sessions in 1984. A Sherman live trap containing a handful of cotton wool and baited with rolled oats was placed at each station. Trapping began in the afternoon and continued for five consecutive days. Traps were opened each day between 1600-1730 hrs and closed the following morning between 0730-1100 hrs to prevent daytime trap mortality. Species, trap number, age (adult or juvenile), sex, weight and tag number were recorded. We used toe clips or aluminum ear tags to identify individuals.

We estimated relative abundance of small mammals as the total num-

ber of individuals captured per trap night (catch/effort) for each ecosite type, area and grid. Abundance was calculated for all small mammals as well as for each individual species.

Small mammal diversity was derived for each area using Patil and Taillie's (1979) diversity profiles. This is a graphic ordering of the diversity of two or more communities. The y-axis represents the percent of small mammals remaining in the sampled population when a species is removed. This is plotted against the number of species that have been removed from the sampled population, with species removal being cumulative.

The profile of an intrinsically more diverse community will plot above that of a less diverse community. If profile lines intersect, then the communities do not differ in diversity.

Vegetation measurements describing microhabitat structure were taken at each station prior to trapping. The characteristics we measured are similar to those reported in other small mammal studies (e.g. Geier and Best 1980, Hallett 1982). These included:

1. Percent canopy cover of grass, forbs, and litter (all downed dead material; e.g. twigs, dead grass, leaves) in a 1.0 X 0.5 m quadrat having the trap station stake as its center;
2. Height (cm) of the nearest shrub (crown foliage >2 dm in diameter) in each quarter around the trap station stake;
3. Line intercept distance (cm) of living and dead shrubs (in the 25 to 50 cm layer above the ground) occurring within two perpendicularly oriented 2-m transects centered at the trap station stake.

Five microhabitat variables were derived from these measurements for analysis. These included: (1) % forb cover, (2) % grass cover, (3) % litter cover, (4) total shrub interception distance (cm), and (5) mean height (cm) of the live shrubs around each stake.

Small mammal abundance data were analyzed using a three-way analysis of variance to determine if



Figure 1.—View from the study site on Badger Mountain, Sheldon National Wildlife Refuge, Nevada.

small mammal abundance differed between areas, years, and ecosites. We used a one-way analysis of variance test to detect differences between areas for individual years and ecosites. To determine the microhabitat preferences of individual species we coded trap locations as being either capture or non-capture stations. We employed a nested two-way analysis of variance to test these preferences among areas and codes, the interaction of areas by codes, and the nested interaction of grids within areas. We considered $P \leq 0.1$ to be significant. Subsequent discussion of small mammal microhabitat selection concerns only the two most abundant species, the deer mouse (*Peromyscus maniculatus*) and the least chipmunk (*Tamias minimus*).

Results and Discussion

Species Composition

Species of small mammals occurring in the two ecosites of our study area are widely distributed throughout

the Great Basin (Hall 1946). These species and their percentage of the total catch were: deer mouse (46.7%), least chipmunk (29.8%), Great Basin pocket mouse (*Perognathus parvus*) (12.3%), sagebrush vole (*Lagurus curtatus*) (7.8%), Townsend's ground squirrel (*Spermophilus townsendii*) (1.2%), golden-mantled ground squirrel (*Spermophilus lateralis*) (1.2%), and long-tailed vole (*Microtus longicaudis*) (0.6%).

Abundance

Total relative abundance of small mammals did not differ between year or area (table 1). However, more animals were captured in the SRH ecosite than in the MR ecosite ($P=0.05$).

There was a general decline in deer mouse ($P=0.08$) and least chipmunk ($P=0.06$) abundance from 1983 to 1984, although this probably reflects the difference in season and length of trapping between the two years. We found no significant difference in abundance for these two spe-

cies between areas or ecosites. This is not surprising given the opportunistic, adaptable, nature of these small mammals. Others have found that heavy grazing in big sagebrush habitat appears to promote an increase in deer mice (Black and Frischknecht 1971, Larrison and Johnson 1973), and least chipmunk numbers (Larrison and Johnson 1973). Hanley and Page (1982) observed a different response for the two species on their big sagebrush-Idaho fescue site 60-80 km west of Badger Mountain. In that study, deer mice were captured in the same numbers in both grazed and ungrazed sites, while least chipmunks were four times more abundant in the grazed site than in the ungrazed site.

Great Basin pocket mice were more abundant ($P<0.01$) in 1983 than 1984, and they were more commonly captured in the SRH ecosite than in the MR ecosite ($P=0.08$). However, there was no significant difference in abundance between the areas. Others have found Great Basin pocket mice to be more abundant on ungrazed big sagebrush sites (Black and Fris-

Table 1.—Abundance of small mammals (number caught per trap night) by year, area and ecosite on the Sheldon National Wildlife Refuge, 1983-84.

Species	Area	Shrubby-Rolling Hills		Mohogany Rocklands	
		1983 #/trapnite(S.E.)	1984 #/trapnite(S.E.)	1983 #/trapnite(S.E.)	1984 #/trapnite(S.E.)
Deer mouse	Excl.	0.081(0.012)	0.047(0.014)	0.061(0.019)	0.050(0.011)
	Allot.	0.063(0.005)	0.052(0.017)	0.064(0.027)	0.018(0.002)
Least chipmunk	Excl.	0.029(0.007)	0.020(0.005)	0.067(0.017)	0.037(0.006)
	Allot.	0.046(0.025)	0.031(0.010)	0.049(0.011)	0.005(0.005)
Great Basin pocket mouse	Excl.	0.013(0.005)	0.028(0.003)	0.003(0.003)	0.029(0.014)
	Allot.	0.011(0.007)	0.031(0.004)	0.005(0.003)	0.014(0.006)
Sagebrush vole	Excl.	0.019(0.010)	0.038(0.020)	0.002(0.002)	0.004(0.004)
	Allot.	0.004(0.003)	0.019(0.004)	0	0
Long-tailed vole	Excl.	0	0.004(0.004)	0	0
	Allot.	0	0.009(0.002)	0	0
Townsend's ground squirrel	Excl.	0	0	0	0
	Allot.	0.005(0.005)	0	0	0.005(0.005)
Golden-mantled ground squirrel	Excl.	0.006(0.006)	0	0.007(0.007)	0
	Allot.	0	0	0	0
Total Catch	Excl.	0.149(0.013)	0.135(0.027)	0.141(0.024)	0.120(0.028)
	Allot.	0.154(0.030)	0.143(0.005)	0.119(0.026)	0.042(0.018)

chknecht 1971), or more abundant on grazed sagebrush sites (Hanley and Page (1982).

Relative abundance of the sagebrush voles and long-tailed voles could not be compared statistically because of the small number of voles captured. There was, however, a general trend for microtine rodents to be more abundant in the SRH ecosite even though grass and forb cover in the MR ecosite were higher. Birney et al. (1976) and Grant et al. (1982) have discussed the importance of cover for microtine rodents in grasslands. Although grass cover was lower in the SRH ecosite, the combination of higher litter cover and shrub intercept in that ecosite may provide better habitat for these rodents. The sagebrush vole was more abundant in the exclosure than in the allotment. Although we were unable to test this trend, it is possible that the sagebrush vole found the exclosure, with its slightly greater grass and shrub cover, to be more inhabitable. It is apparent from other studies that grass and shrub cover are important components of sagebrush vole habitat (MacCracken et al. 1985, Maser et al. 1974, Maser and Strickler 1978, O'Farrell 1972).

Diversity

In 1983, diversity of small mammals in the exclosure was greater than in the grazing allotment (fig. 2). Relative abundance of deer mice, the most common species (table 1), was similar in both areas; however, we caught one more species in the exclosure. In 1984, small mammal diversity was greater in the allotment than in the exclosure. During that year, deer mice made up a somewhat smaller relative proportion of the small mammal total in the allotment (table 1); thus the line for the allotment starts higher on figure 2 indicating greater evenness in the percentage each species contributed to the population. We captured one

more species in the allotment than in the exclosure which extended the tail of the profile further to the right. Because of this change from one year to the next, we were unable to conclude what impact the grazing system had on small mammal diversity. Hanley and Page (1982) observed a higher diversity index on their ungrazed

sagebrush-Idaho fescue site 60-80 km west of Badger Mountain.

Vegetation on the Small Mammal Study Area

Generally, the SRH ecosite had lower grass and litter cover and a greater

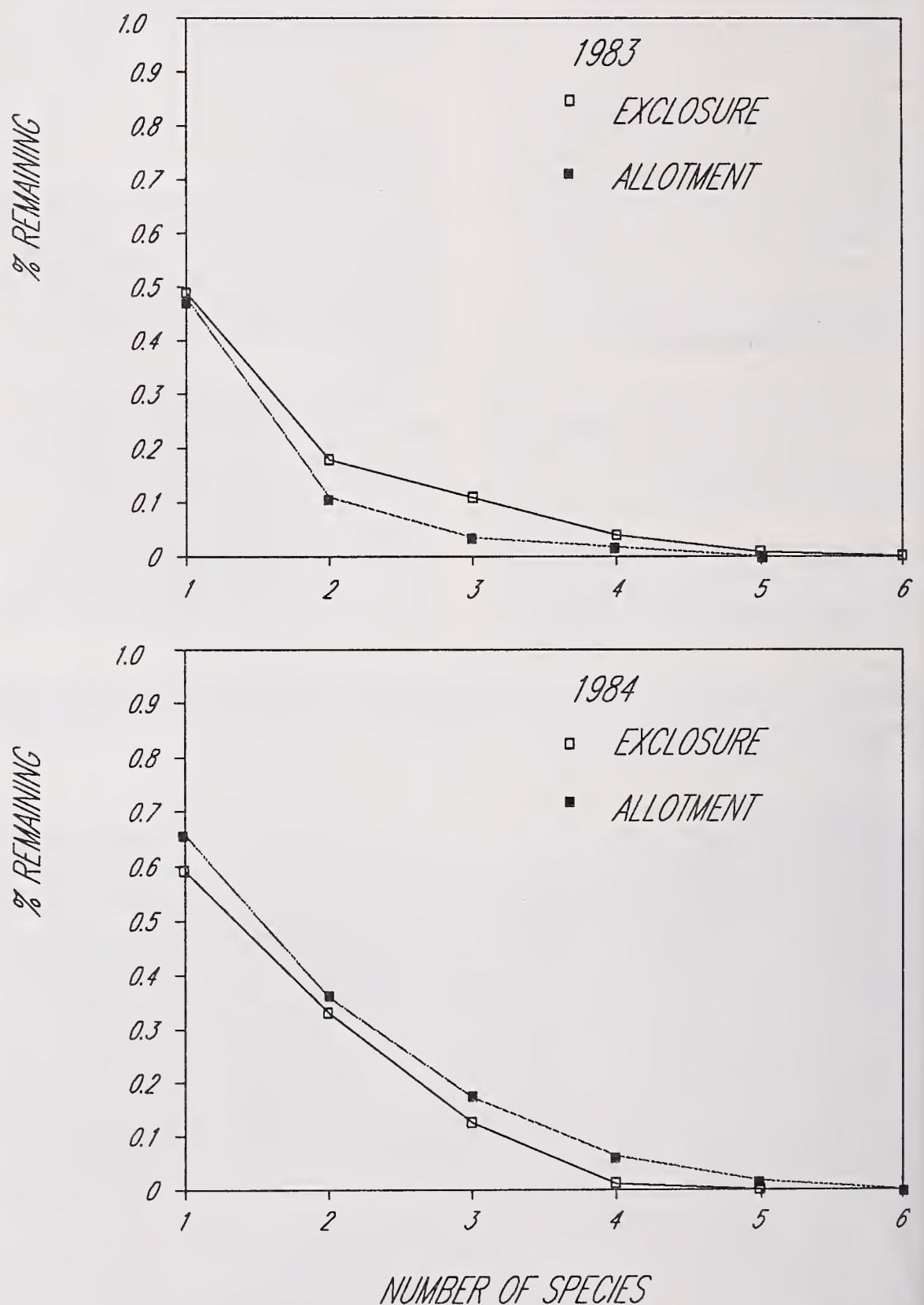


Figure 2.—Small mammal diversity profiles for the cattle exclosure and the allotment, Sheldon National Wildlife Refuge, 1983-84. If profile lines intersect, then diversity does not differ between areas (Patil and Taillie 1979).

shrub intercept value than did the MR ecosite (fig. 3). In the SRH ecosite, microhabitat characteristics did not differ between the enclosure and allotment, except for 1983 when shrub height in the allotment was lower ($P < 0.05$) than that in the enclosure.

In the MR ecosite, shrub intercept was lower ($P < 0.03$) in the allotment than in the enclosure both years and grass cover was higher ($P < 0.10$) in the enclosure in 1983. In both ecosites, there was a general trend for cover of both grasses and forbs to

be lower in the allotment than in the enclosure.

This trend is probably due to the cattle grazing. However, the fact that the means are relatively similar (especially in the SRH ecosite) and do not differ significantly between areas indicates that the grazing effect is within goals established by the refuge.

Microhabitat Characteristics of Deer Mice Catch Sites

In the SRH ecosite, traps where deer mice were caught had significantly greater litter cover ($P = 0.07$ in 1984), shorter shrubs ($P = 0.09$ in 1984), and greater shrub intercept ($P = 0.10$ in 1983) than traps where deer mice were not caught (fig. 4). These patterns tended to hold for both years.

In the MR ecosite, litter cover, which is greater than in the SRH ecosite, did not appear to be a significant vegetative characteristic (fig. 4). Grass cover in 1984 was lower ($P = 0.06$) and shrub height ($P = 0.02$) and shrub intercept ($P = 0.08$) were greater at traps where deer mice were caught than where they were not caught.

In both the SRH and MR ecosites, deer mice appeared to use microhabitat that had greater shrub intercept. This corresponds with the findings of Feldhamer (1979) who noted an increase in deer mouse density with increased foliage in the shrub layer. Other studies have found that deer mice were associated with light cover in heavily grazed sites (Black and Frischknecht 1971), with increasing forb cover (Geier and Best 1980), or with no measured habitat variable (Hallett 1982).

Microhabitat Characteristics of Chipmunk Catch Sites

In the SRH ecosite, shrub height was lower ($P < 0.08$ in 1984) in catch locations in the enclosure and the allot-

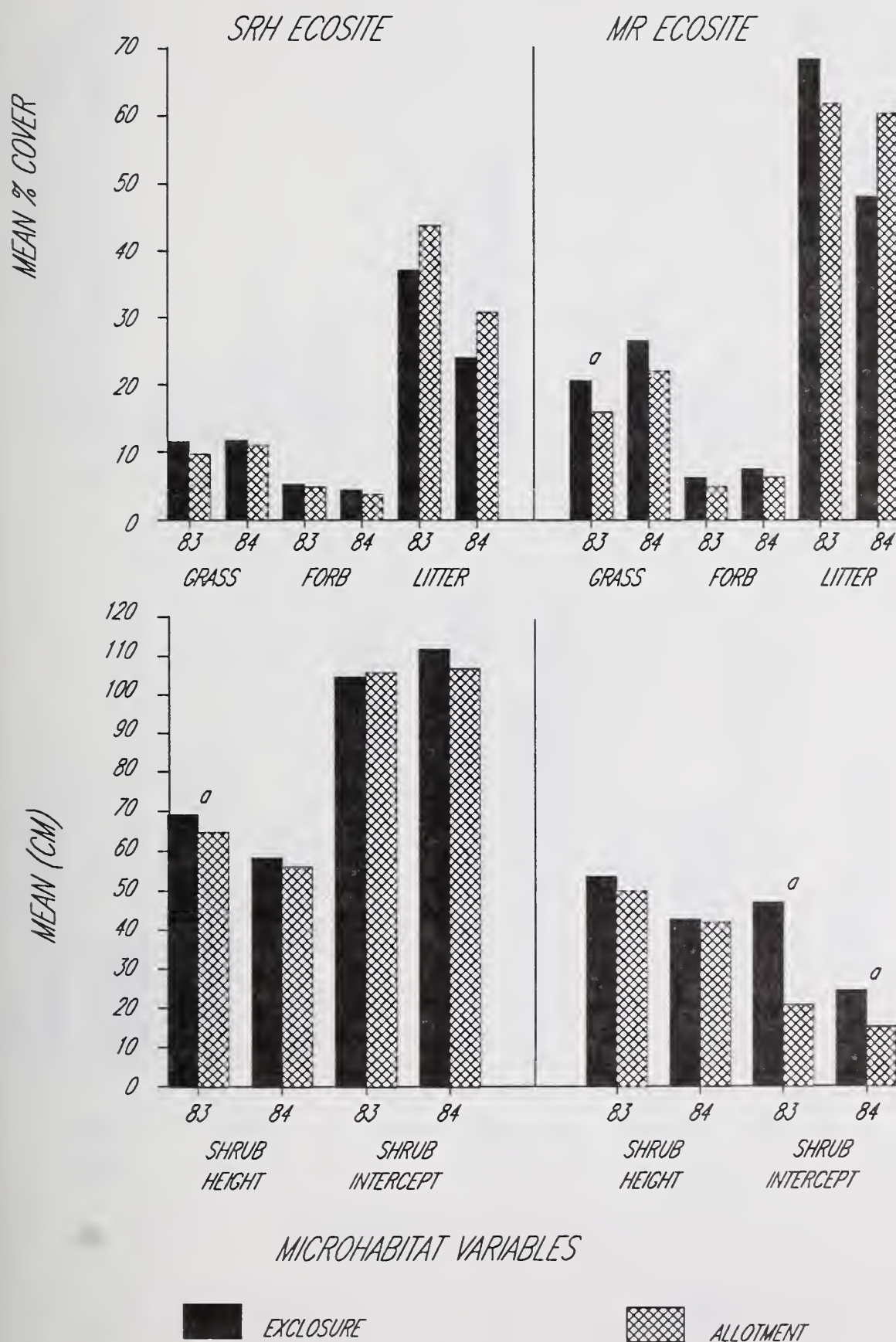


Figure 3.—Microhabitat characteristics around trap stations in the shrubby-rolling hills and mahogany rocklands, Sheldon National Wildlife Refuge. Variables with an "a" denote a P value of < 0.1 between the two areas.

ment than in non-catch locations. This pattern held in 1983 (fig. 5).

In the MR ecosite there were no consistent patterns of chipmunk microhabitat use (fig. 5). Shrub interception, in 1984, was greater ($P < 0.05$) in chipmunk catch locations than non-catch locations; however this pattern was not evident in 1983.

Microhabitat selection by the least chipmunk lacked a consistent pattern for either ecosite or year. However, the fact that the least chipmunk is an opportunistic forager and is the most widespread of all North American chipmunks (Hall 1981), suggests that this rodent adapts rapidly to a variety of habitat types. Sullivan (1985) found that the least chipmunk was associated with a wide variety of ecological situations in the southwest and suggested that this species may be predisposed to exploiting marginal environments.

Conclusions

These results indicate that the grazing regime initiated on the Badger Mountain allotment had no discernible impact on the relative abundance and diversity of small mammals, four and five years after its implementation. The dominance of two opportunistic species on the study area probably contributed to this lack of difference. We suggest future monitoring of the study area to determine the long-term response of small mammals to the grazing program. Particular attention should be given to the two vole species which are the most sensitive to changes in cover.

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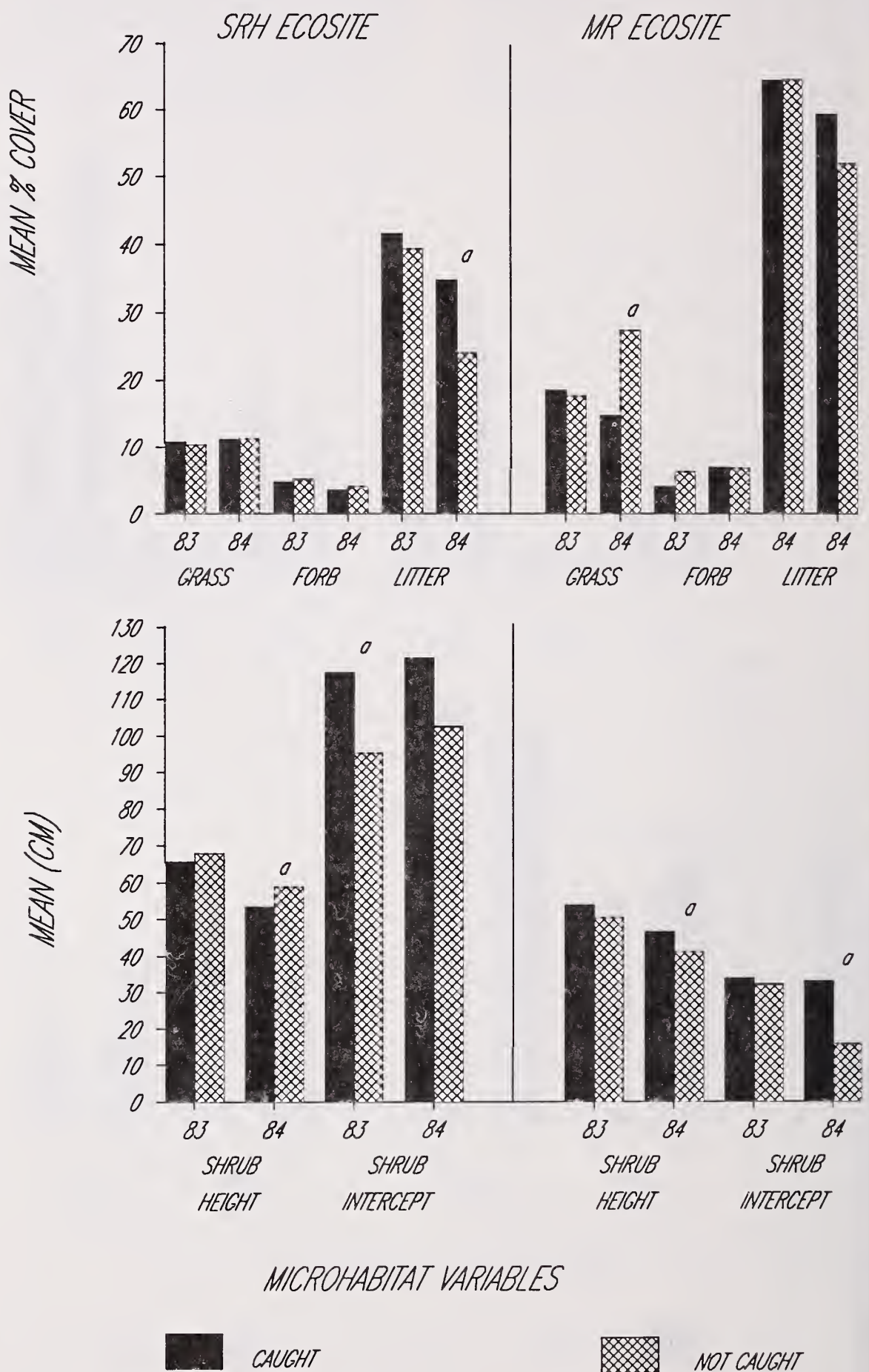


Figure 4.—Microhabitat characteristics around traps where deer mice were captured and not captured by year and ecosite, Sheldon National Wildlife Refuge. Variables with an "a" denote a P value of < 0.1 between the two areas.

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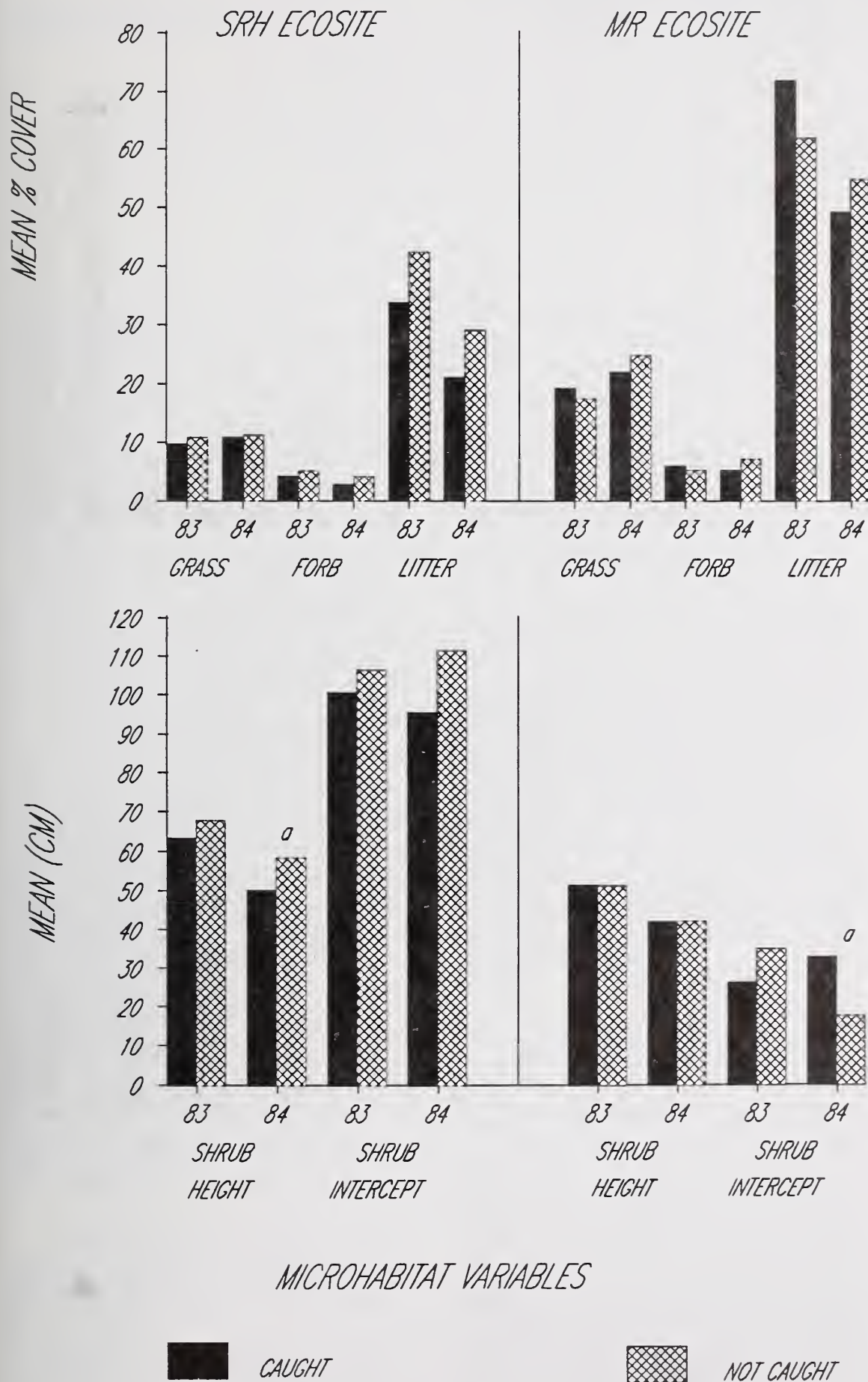


Figure 5.—Microhabitat characteristics around traps where least chipmunks were captured and not captured by year and ecosite, Sheldon National Wildlife Refuge. Variables with an "a" denote a P value of <0.1 between the two areas.

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Effect of Seed Size on Removal by Rodents¹

William G. Standley²

Seeding is commonly used for restoring depleted vegetation. Many seeding projects fail because rodents eat the seeds (Bramble and Sharp 1949, Spencer 1954, Nelson et al. 1970). A variety of techniques for reducing the impact of rodents have been tested, but few have been successful. Most often resource managers poison rodent populations before seeding, but this method is largely unsuccessful because of rapid immigration of new individuals (Sullivan 1979, Sullivan and Sullivan 1984). New methods of biological management could be developed that use information gained from diet and behavior studies to reduce destruction of seeds by rodents. Many studies show that certain rodents prefer particular species or sizes of seeds (Reynolds and Haskell 1949, Reynolds 1950, Abbott 1962, Gashwiler 1967, Smith 1970, Lockard and Lockard 1971, Smigel and Rosenzweig 1974, Everett et al. 1978, Price 1983). Thus, whenever alternative plant species are available that both meet the resource manager's objectives and have seeds not preferentially foraged by local seed-

eating rodents, seeding could be successful even with rodents present.

In southwestern deserts of North America, where range managers are attempting to restore rangelands depleted by overgrazing (Cox et al. 1982), kangaroo rats (*Dipodomys* sp.) and pocket mice (*Perognathus* sp. and *Chaetognathus* sp.) are some of the primary seed eaters (Brown et al. 1979b). As early as 1950, Reynolds suggested that the influence of Merriam's kangaroo rats (*Dipodomys merriami*) on seeding success depends on the size of seeds used. Brown et al. (1979b), Inouye et al. (1980), and Price (1983) all found that heteromyids preyed selectively on large seeds. In this study, I investigated the prediction that fewer small seeds than large seeds would be removed by rodents in a seeded area in southeastern Arizona.

Study Area and Methods

The study area was on the USDA Forest Service Santa Rita Experimental Range located 45 km south of Tucson, Pima County AZ, which is thoroughly described by Martin and Reynolds (1973). The vegetation was typical Sonoran desert-scrub, dominated by mesquite (*Prosopis juliflora*), burroweed (*Haplopappus tenuisectus*) and cholla (*Opuntia* spp.). Annual precipitation averages 36 to 43 cm and is bimodal, with peaks in winter and summer. Plots were seeded fol-

Abstract.—Plots located in southeastern Arizona were seeded with small and large grass seeds. After 3 days, virtually all large seeds were removed by rodents, while small seeds were still present 36 days after planting. Thus, managers may increase seed survival in this area, without removing rodents, by seeding with small seeds rather than large seeds.

lowing all recommended procedures (Jordan 1981), using large and small seeds, both separately and together. Seeded plots were located within a slightly sloped 1-hectare area with a Comoro soil type, at an elevation of 1300 m. I compared the number of seeds surviving on 4 experimental plots to the number of seeds surviving on a control plot which was protected from rodents.

The study area was prepared by removing large shrubs by hand and plowing small plants with a disk. The control plot was protected from rodents with a rodent-proof fence similar to that used by Brown et al. (1979a). All rodents within the enclosure were removed by trapping before seeding. Each of the 5-15 x 17 m plots was seeded with 3 evenly placed pairs of 15 m rows, one pair for each of 3 treatments which were: (1) small seeds planted at a rate of 175/m (0.15 g/m), (2) large seeds planted at a rate of 100/m (4.7 g/m), and (3) 5 small and large seeds planted together at 88/m and 50/m (0.07g/m and 2.35 g/m), respectively. Seeding rates were chosen according to recommended rates for similar sized seeds (Jordan 1981). The treatment assigned to each pair of rows was randomly selected. The small seeds were blue panicgrass (*Panicum antidotale*) which weighed an average of 0.85 mg each. The large seeds were barley (*Hordeum vulgare*) which weighed an average of 47.0 mg each. All seeds were planted with

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a cone seeder at a depth of 1 to 2 cm on 21 June 1984, just before expected summer rains. Because blue panicgrass seeds are very small and difficult to recover from the soil, they were dyed with water soluble green food coloring before planting. Barley seeds were also dyed to avoid a possible bias.

The species of rodents on the experimental plots were monitored by placing 100 live traps at 10 m intervals on and around the plots on the 5th and 6th nights after planting. Traps were baited with a mixture of both sizes of seeds and checked at midnight and sunrise.

The number of seeds surviving on plots was monitored by collecting soil samples from the rows immediately after planting and at 3, 9, 18, and 36 days after planting. One random sample was taken from each quarter of every row each time. Samples were not taken from the outer meter of any row because the cone seeder applied seeds at a more variable rate at the beginning and end of each row.

Soil samples, 2.5 to 3.5 cm deep and 15 x 25 cm in area, were taken lengthwise along each row with the aid of a two-sided, fixed-area sampler and a trowel. The samples were placed in paper bags, and oven-dried at 50 C for 24 hours. Seeds were recovered by shaking soil samples through a series of Tyler sieves (#5, #10, #14, #18, #20, and #25) for 3 minutes. The number of seeds remaining were counted by examining the contents of each sieve, both dry and immersed in a salt water solution, through a 10X viewing scope.

The average number of seeds recovered in the soil samples taken from the 4 experimental plots divided by the total number found in the control plot times 100 was used as a seed survival index (SSI). This dimensionless index permits comparison of the removal of different sized seeds by rodents even though they were planted at different rates. It also standardizes for the experi-

mental error contributed by the difficulty of recovering small seeds. The granivorous arthropods and birds present on the study area had equal access to control and experimental plots, so should not have biased SSIs.

Results

Eleven of 17 individual rodents captured on or around the plots were heteromyids: 9 were Merriam's kangaroo rats, and 2 were bannertail

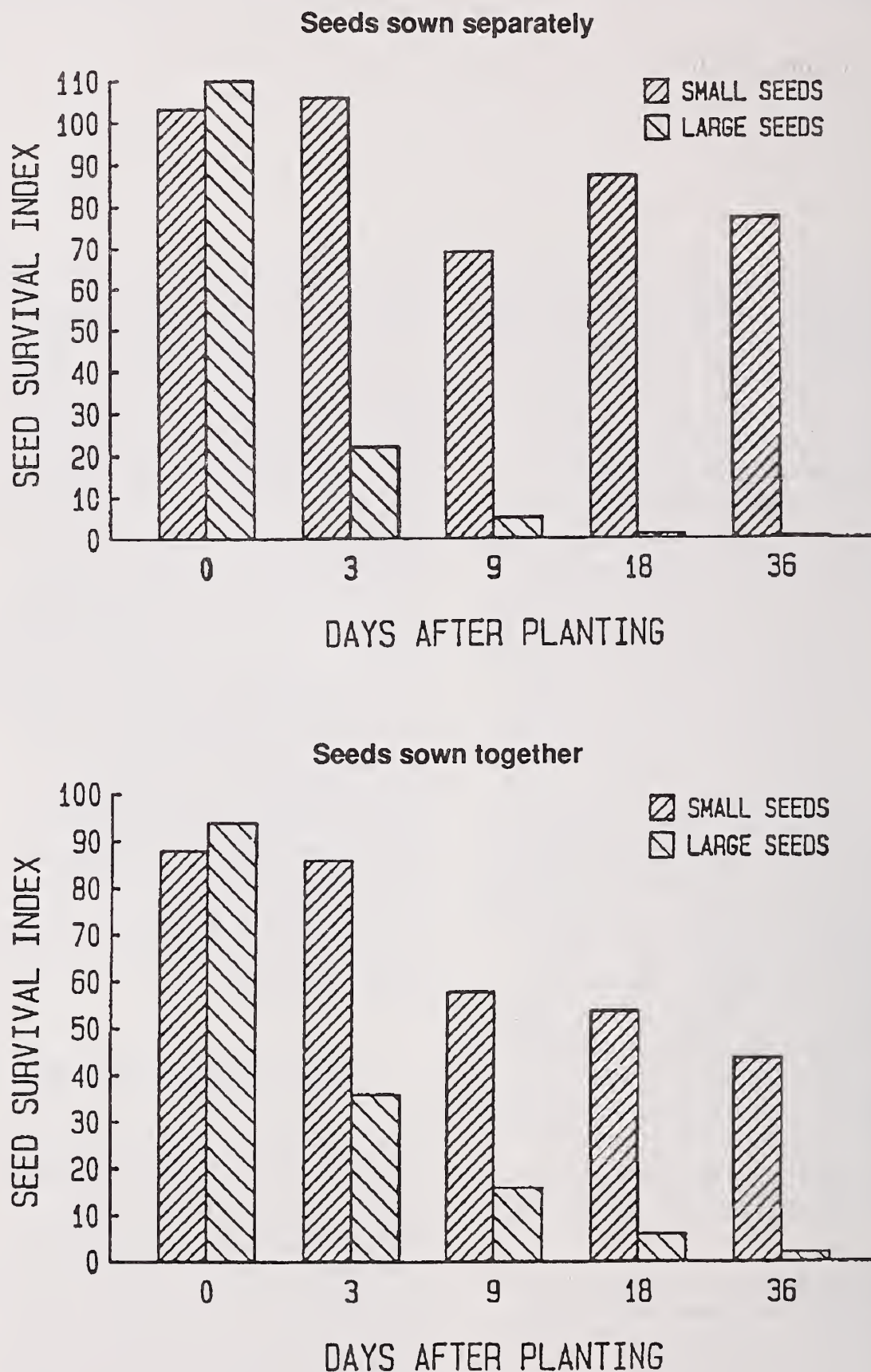


Figure 1.—Seed survival index (average number of seeds recovered in 4 experimental plots divided by total number of seeds recovered in the control plot times 100) for small and large seeds. (A) Seeds sown separately and (B) Seeds sown together.

kangaroo rats (*D. spectabilis*). Two white-throated woodrats (*Neotoma albigula*), 2 southern grasshopper mice (*Onychomys torridus*), 1 deer mouse (*Peromyscus maniculatus*) and 1 cotton rat (*Sigmodon hispidus*) were also captured.

Whether large and small seeds were planted separately or together, the SSIs were higher for small seeds than for large seeds starting with 3 days after planting (fig. 1). After 36 days, the large seeds planted either separately or with small seeds were virtually gone from experimental plots (SSI = 0.4 and 2.1, respectively). The SSI for small seeds planted separately was 76.5 after 36 days, while the small seeds planted with large seeds had an SSI of 43.6. The SSIs of large seeds planted separately decreased at a faster rate than the SSIs of large seeds sown with small seeds. The SSIs of small seeds planted separately decreased at a slower rate than the SSIs of small seeds sown with large seeds, however. Complete data are presented in Standley (1985).

Discussion

I do not present inferential statistics to test for significant differences between large and small seed survival because the experimental plots were actually sub-plots rather than true replicates (Hurlbert 1984). For this study site, however, striking differences between the SSIs of large and small seeds whether planted separately or together are certainly evidence that smaller seeds have a much higher survival rate than large seeds due to differential predation by rodents.

The higher rate of removal of large seeds planted separately compared to large seeds planted with small seeds may have occurred because the lower density of large seeds in the mixed rows made them less attractive to rodents. The relatively higher rate of removal of small seeds planted with large seeds, compared

to small seeds planted separately, likely occurred because large seeds attracted rodents to the rows, where the rodents then ate both sizes of seeds. Sullivan and Sullivan (1982) observed the opposite effect when seeding lodgepole pine (*Pinus contorta*). Lodgepole seed consumption by rodents was reduced by planting the relatively small lodgepole seeds with sunflower seeds, which were larger and more preferred by granivorous rodents present. The opposing results may be due to differences in method of seeding (Sullivan and Sullivan broadcast their seeds) or the size of plots (Sullivan and Sullivan's plots were larger). Another possibility is that the main granivorous rodents in their study area, deer mice, are more selective than the heteromyids present in this study. Nine days after planting there was a lower SSI for small seeds planted separately (fig. 1a) than on 18 or 36 days, which can only be attributed to variability in seeding rate and sampling error.

It is possible that not all seeds removed by rodents, small or large, were destroyed. Reynolds and Glendening (1949) found that the seed caching behavior of Merriam's kangaroo rats actually increased spread of some plant species.

Factors other than seed size affect selection by rodents for particular seed species, such as percent soluble carbohydrates (Kelrick and MacMahon 1985, Kelrick et al. 1986; but also see Jenkins 1988), moisture content (Frank 1988a), and moldiness (Frank 1988b). For most seeds, however, resource managers have only the information on size available. This study only compared the effect of size by using grass seeds of similar composition that differ most in their linear dimensions. The results of this study support other studies which showed that heteromyid rodents selected large seeds and reduced standing stocks of large seeds in the soil to a greater extent than small seeds (Brown et al. 1979a, Inouye et al.

1980, Price 1983). Therefore, when site conditions and management needs allow a choice of which species to seed, resource managers should consider the size of seeds when planning seeding in areas inhabited by heteromyids.

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Habitat Use by Gunnison's Prairie Dogs¹

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and Clark Schaack⁴

Abstract.—Gunnison's prairie dogs (*Cynomys gunnisoni*) are social, colonial mammals found in Colorado, New Mexico, and Arizona. Colony location depends to a great extent on the distribution and abundance of plants used as food. Colonies with the highest densities of prairie dogs occur in habitats where there is a high abundance of native species of plants. From a management standpoint, prairie dog populations can be conserved by maintaining habitats that offer such resources.

Prairie dogs often have been considered "weedy" species that thrive in disturbed habitats. However, uncertainty remains about the impact of prairie dogs on their habitat, and about their economic impact as competitors of domesticated herbivores. Some studies of primarily black-tailed prairie dogs (*Cynomys ludovicianus*) show that they have a negative effect on their habitat, while other studies show a positive effect. Negative effects include decreased forb and grass cover in prairie dog towns (Knowles 1982, Archer et al. 1984), higher silicon concentrations in grasses found in areas grazed by prairie dogs (Brizuela et al. 1984), and removal of plant biomass that could be utilized by cattle (Crocker-Bedford 1976, Hansen and Gold 1977, Crocker-Bedford and Spillett 1981). Positive effects include increased plant species diversity in prairie dog towns (Lerwick 1974, Boddicker and Lerwick 1976, Gold 1976, Severe 1977, Beckstead and

Schitoskey 1980, Fagerstone 1981, Archer et al. 1984); greater production of forbs and grasses (Uresk and Bjugstad 1980, Agnew 1983); and better quality food and growing conditions inside prairie dog towns (Hassien 1976, Beckstead and Schitoskey 1980, Fagerstone 1981, Coppock et al. 1980, 1983a, 1983b, Detling and Painter 1983). Prairie dog colonies have also been shown to provide habitat for many different species of vertebrates other than prairie dogs (Campbell and Clark 1981, O'Meilia et al. 1982, Agnew 1983, Clark et al. 1982).

The economic effects of prairie dogs are also currently unclear. Although they are considered pests (Uresk 1985), a series of studies has shown that controlling or eradicating prairie dogs has little effect on increasing the amount of food available for cattle (Crocker-Bedford 1976, Klatt and Hein 1978, Collins et al. 1984, Uresk 1985), and experimental studies of competition between prairie dogs and steers failed to show that the prairie dogs had any significant negative impact on the weight of the steers (O'Meilia et al. 1982).

Prairie dogs have been characterized as being oriented to disturbed sites that are overgrazed by cattle or buffalo (Osborn and Allan 1949). The relationship between prairie dog occurrence and overgrazing, however, is a correlational one: prairie dogs can be found at sites that are overgrazed by large herbivores, but this

does not necessarily imply that the prairie dogs specialize in colonizing sites that are overgrazed. Overgrazing might be occurring subsequent to colonization. For example, bison are attracted to prairie dog towns as grazing sites, because the vegetation associated with such towns may be more digestible, and have a higher nitrogen content than the vegetation at sites not colonized by prairie dogs (Coppock et al. 1983a, 1983b).

Disturbance of a habitat can be provided by the activities of the prairie dogs themselves. By digging extensive burrow systems (King 1984), prairie dogs disturb soil, promoting the growth of disturbance-oriented vegetation and increasing plant diversity (Gold 1976; Hansen and Gold 1977). Because prairie dogs have a system of vigilance that depends on being able to see terrestrial predators from some distance away (Slobodchikoff and Coast 1980), they clip shrubs and other tall vegetation that impede visual detection. This in turn alters the habitat into one that has predominantly short grasses and annual forbs, rather than the taller grasses and shrubs that are more characteristic of climax communities (Koford 1958).

The goal of this paper is to evaluate habitat use by Gunnison's prairie dogs (*Cynomys gunnisoni*), and to consider this habitat use in the context of managing existing populations of this species. Many previous

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ecological studies of prairie dogs have focused on the blacktailed prairie dogs (*Cynomys ludovicianus*) found in the midwestern states. Gunnison's prairie dogs offer a better opportunity to evaluate habitat requirements, because this species is associated with habitats that have been modified less by man than habitats where blacktailed prairie dogs are currently found.

In an attempt to establish some common habitat conditions that are preferred by Gunnison's prairie dogs, we have examined the following factors at several prairie dog sites: (1) burrow density as an indicator of prairie dog population density; and (2) plant diversity, evenness, cover, and proportions of native and introduced species.

Study Areas

Seven colonies in the vicinity of Flagstaff, Arizona, were investigated. These were: (1) Humane Society (HS), within the city limits at an elevation of 2250 m, in a meadow surrounded by Ponderosa pine (*Pinus ponderosa*) trees on three sides and a heavily-utilized dirt road on the remaining side; (2) Denny's (D), also within the city limits at an elevation of 2250 m, in a small meadow encircled by a traffic loop that serves as an approach to the I-17 freeway; (3) Snow Bowl (SB), 10 km north of Flagstaff in an old-field pasture at an elevation of 2400 m; (4) Upper Michelbach (UM), on a privately owned ranch 20 km north of Flagstaff at an elevation of 2650 m; (5) Lower Michelbach (LM), also at 2650 m and located within 1 km east of UM; (6) Potato Lake (PL), in an alpine meadow surrounded by forested slopes, 25 km northeast of Flagstaff at an elevation of 2850 m; and (7) Bismark Lake (BL), another alpine meadow 20 km northeast of Flagstaff at 2900 m.

Grazing pressure on these sites varied. The most heavily grazed site was Upper Michelbach, with grazing

levels of 0.8 ha per AUM. The Humane Society site was heavily grazed (1.2 ha per AUM) until 1978, after which there was no grazing. Both Lower Michelbach and Snow Bowl had the same level of grazing (6 ha per AUM). The Potato Lake and Bismark Lake sites had relatively light levels of grazing (12 ha per AUM at PL; 14 ha per AUM at BL). The Denny's site was not grazed at all in the last 20 years (all grazing information from J. Mundell, pers. comm.).

Methods

To estimate relative densities of prairie dog populations, we sampled burrow densities at six of the sites (HS, SB, UM, LM, PL, and BL). Burrows were estimated by laying out twelve 50 m transects, and counting all the burrows that were within 0.5 m of each side of the transect line. Based on the counts of burrows per transect, mean numbers of burrows / 0.005 ha (mean number of burrows per 50 m-sq) were calculated for each colony. Because of the small size of the colony at BL, only six transects were used there. Although this method did not provide a total number of burrows per site (a number constantly changing depending on prairie dog construction activity), it did provide a measure that allowed comparison of the six sites.

As an estimate of habitat composition, vegetation at five sites (HS, SB, D, PL, and BL) was sampled from May-October, 1986-87. All plant species found at each site were identified to species and classified as native non-weedy, native-weedy, or introduced-weedy. Reference specimens for each species from each site have been deposited in the Herbarium at Northern Arizona University.

For estimates of plant diversity and percent cover, we sampled plants every month along transects at two sites (HS and SB) from May-October, 1986 and 1987. Each site had six 100 m parallel transects spaced 20

m apart. Presence or absence of plants by species were recorded every 2 m along each transect.

Similarity indices (SI) were calculated for plant species composition between sites, as follows:

$$SI = \frac{\text{Number of Species Common to Both Site A and B}}{\text{Total Number of Species in Site A + Site B}}$$

This is an index that allows comparisons of sites based on the percentage of species common to the two.

Prairie dog densities were determined at two sites, HS and SB, by actual counts of all the animals at each site. The prairie dogs were trapped weekly in squirrel-sized Tomahawk live traps and marked with hair dye. Movements of marked prairie dogs were observed and plotted with respect to a 100 x 120 m grid of stakes set up 10 m apart. Territories were determined behaviorally, on the basis of aggressive behaviors such as chases between interterritory members, and cooperative behaviors such as greet-kisses between intraterritory members. At these two sites, HS and SB, the number of burrows in each territory was counted.

All statistical analyses were done on a Honeywell Sigma 6 mainframe computer, using SPSS statistical packages (Nie et al. 1975). Analyses included regression, correlation, analysis of variance, and least significant difference. Additionally, ecological indices were calculated: evenness, percent cover, Simpson's dominance, Shannon-Weaver diversity, and H max (Poole 1974).

Results

Plant Species Composition

Similarity indices show that some sites were quite dissimilar from other sites (table 1). The HS and D sites were most similar (63.7 percent similarity), and SB was fairly similar to

Table 1.—Similarity indices for five Gunnison's prairie dog colonies, based on plant species composition at each site. A similarity of 100 implies that all the plant species at both sites are the same. A similarity of 0 implies that no plant species are common to the two sites. Sites are: BL = Bismark Lake; D = Denny's; PL = Potato Lake; SB = Snow Bowl; HS = Humane Society.

Site	BL	D	PL	SB
Humane Society (HS)	6.7	63.7	8.6	54.1
Snow Bowl (SB)	10.2	44.1	12.9	—
Potato Lake (PL)	23.4	4.8	—	—
Denny's (D)	8.2	—	—	—

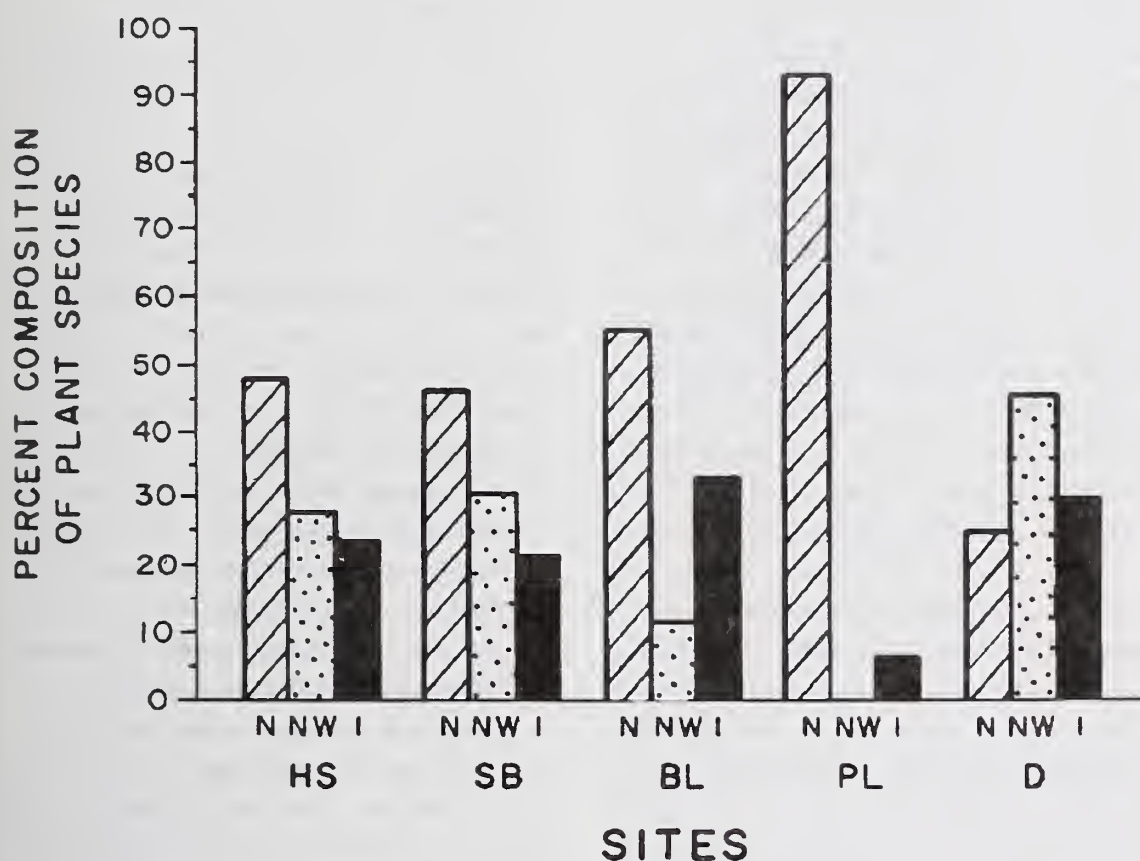


Figure 1.—Composition of plant species at five Gunnison's prairie dog colonies near Flagstaff, Arizona. Percentages shown are for Native-nonweedy species (N), Native-weedy species (NW), and Introduced-weedy species (I). Sites are: HS = Humane Society; SB = Snow Bowl; BL = Bismark Lake; PL = Potato Lake; D = Denny's.

Table 2.—Mean burrow densities and standard deviations at 6 Gunnison's prairie dog colony sites. Means that are not significantly different (LSD Test) are associated by the same letter.

Site	Mean + SD	LSD Test
Upper Michelbach (UM)	5.42 + 2.15	a
Humane Society (HS)	4.17 + 1.90	a b
Snow Bowl (SB)	3.17 + 1.59	b c
Lower Michelbach (LM)	2.92 + 2.47	b c
Potato Lake (PL)	2.83 + 1.64	b c
Bismark Lake (BL)	2.17 + 1.72	c

the HS site (54.1 percent similarity) and to the D site (44.1 percent similarity). The HS, D, and SB sites were quite dissimilar from the other two sites, PL and BL, and the two latter sites had a low level of similarity (23.4 percent) to each other.

The five sites differed in plant species composition based on the proportion of native-nonweedy, native-weedy, and introduced-weedy plant species (fig. 1). The PL site had the greatest proportion of native-nonweedy species (93.1 percent), and the D site had the lowest (27.2 percent). Conversely, the PL site had no (0 percent) native-weedy species, while the D site had the highest proportion (45.7 percent) of native-weedy species. The BL site has the greatest proportion (33.3 percent) of introduced-weedy species found at any site.

Prairie Dog Burrow Density

The mean numbers of burrows per 0.005 ha found at sites HS, SB, UM, LM, PL, and BL are shown in table 2. The highest burrow density was at UM, and the lowest density was at BL. These differences between sites were significant ($LSD = 1.62, P = 0.05$). The two sites from the Michelbach colonies (UM and LM) had significantly different burrow densities, even though these two sites were within 1 km of one another.

Burrow density was positively correlated with prairie dog density at both sites (HS and SB) where prairie dog densities were determined and all burrows were counted. Burrow density significantly correlated with prairie dog density at $r = 0.665$, accounting for 44.2 percent of the variance ($F = 10.32, df = 1, 13, P < 0.01$).

For a pooled 15 territories at the two sites, the mean burrow density was 13.73 burrows per territory ($s = 8.3$), and the mean number of prairie dogs per territory was 6.4 ($s = 6.7$). Consequently, on the average, there were twice as many burrows as prairie dogs per territory.

Burrow Density, Evenness, Plant Cover, and Plant Species Diversity

Plant cover and plant species diversity were negatively correlated with burrow density. Multiple regression analysis with burrow density as the dependent variable and plant evenness, percent cover, Simpson's dominance, Shannon-Weaver diversity, and H_{\max} as independent variables was significant ($F = 5.25$, $df = 5, 7$, $P < 0.05$), accounting for 88.8 percent of the total variance in burrow density. Of these, evenness ($F = 7.47$), percent cover ($F = 10.37$), and Shannon-Weaver diversity ($F = 7.39$) were significant to the regression. Evenness had an $r = -0.416$, percent cover had an $r = -0.349$, and Shannon-Weaver diversity had an $r = -0.427$.

Burrow Density, Native Species, and Introduced Species

Burrow density was negatively correlated with the number of introduced-weedy plant species ($F = 18.14$, $df = 1, 10$, $P < 0.01$). Regression analysis showed that burrow density was correlated with introduced-weedy plant species at $r = -0.673$, accounting for 45.3 percent of the variance in burrow density.

Burrow density was not significantly correlated with either native-nonweedy species or native-weedy species when each of these was considered as an independent variable. However, when these two were combined into a single variable, native species, this produced a highly significant positive correlation of $r = 0.803$ ($F = 18.14$, $df = 1, 10$, $p < 0.01$), accounting for 64.5 percent of the variance in burrow density.

Burrow Density, Plant Species, and Levels of Grazing

Burrow density was significantly correlated with the level of grazing ($r =$

0.903 , $F = 17.8$, $df = 1, 4$, $P < 0.05$). The more a site was grazed, the higher was the burrow density. Regression analysis showed that grazing levels were not significantly correlated with either the number of introduced species or the number of native nonweedy species at a site. Grazing was significantly correlated with the number of native weedy species ($r = 0.975$, $F = 37.9$, $df = 1, 2$, $P < 0.05$), and weakly correlated with the total number of plant species ($r = 0.947$, $F = 17.4$, $df = 1, 2$, $P = 0.06$). Multiple regression with burrow density as the dependent variable and native species, introduced species, and grazing level as independent variables showed that native species (number of native weedy and native nonweedy species combined) explained 97.9 percent of the variance in burrow density, while grazing level explained an additional 1.8 percent and introduced species explained 0.2 percent.

Discussion

Our results show that Gunnison's prairie dogs thrive at sites with native-nonweedy and native-weedy species of plants. Gunnison's prairie dogs apparently do not prefer sites that have a high proportion of introduced-weedy species. This is not surprising when one considers the dietary requirements of these animals. Shalaway and Slobodchikoff (1988) found that the diet of Gunnison's prairie dogs at three sites in the Flagstaff area consisted primarily of native plants: native-weedy and native-nonweedy species made up 60-80 percent of the animals' food. Introduced-weedy species made up a relatively low proportion of the diet of Gunnison's prairie dogs in that study.

Contrary to the findings of studies with blacktailed prairie dogs (Lerwick 1974, Boddicker and Lerwick 1976, Gold 1976, Hansen and Gold 1977, Beckstead and Schitoskey 1980,

Archer et al. 1984), Gunnison's prairie dogs did not increase plant species diversity, but instead decreased it. This effect can be produced by the clipping action of prairie dogs on plants that tend to grow tall and obscure the animals' view of terrestrial predators. Such clipping action can lower the competitive ability of shrubs and other tall plants, eventually eliminating them from prairie dog towns. Many of these species are introduced weedy plants. A similar effect was described by Clements and Clements (1940) with Gunnison's prairie dogs.

The effects of Gunnison's prairie dogs on plant cover were consistent with those found by other studies (Knowles 1982, Archer et al. 1984). In each case, prairie dogs decreased plant cover. This is to be expected, since all species of prairie dogs graze on vegetation and can eat up some 24-90 percent of the primary production of a site (Osborn and Allan 1949, Hansen and Gold 1977, Crocker-Bedford and Spillett 1981). To the extent that blacktailed prairie dogs and cattle have a dietary overlap of 76 percent (Kelso 1939), prairie dogs have been construed as competitors of large herbivores such as cattle. However, because prairie dogs feed very selectively on plants, 80 percent of the biomass they ingest may come from plant parts not utilized by cattle (Crocker-Bedford 1976). Also, any potential competitive effect might be minimized by the relatively small size of most extant prairie dog colonies (King 1955; Koford 1958; Smith 1955), and the beneficial effects that large herbivores may obtain from plants that grow in prairie dog colonies (Coppock et al. 1983a).

The positive correlation between grazing level and density of prairie dog burrows suggests that prairie dogs are found more in habitats that are highly grazed. However, merely addressing prairie dog management in terms of possible competition with cattle misses a much more fundamental issue: that of the prairie dog's

place in a natural ecosystem. While our study has found a positive correlation between prairie dog densities and grazing, the presence of these animals at ungrazed sites indicates that they can establish themselves in ungrazed areas that have the right configuration of habitat characteristics.

A much more important point than grazing is the strong link between the presence of prairie dogs and the success of native species of plants. Introduced weeds are not favored in prairie dog colonies, even though the soil is disturbed through the burrowing actions of these animals. Rather than being "weedy" pests who come into overgrazed lands, prairie dogs might actually have the function of repairing overgrazed land, and driving the plant community toward a more natural one.

The mechanism for how prairie dogs might drive the ecosystem toward more native plant species is still unclear. We have found that Gunnison's prairie dogs decrease both species diversity and plant cover. The decrease in species diversity apparently comes from a decrease in the component represented by the introduced weedy plant species, and not from the native plant species. The decrease in plant cover comes from herbivory on the plants growing in the colonies. Some native plant species produce more flowering stalks and more seeds when they are grazed by herbivores (Paige and Whitham 1987). Experimental evidence for black-tailed prairie dogs shows that both forbs and grasses increased in plots that contained both prairie dogs and cows (Uresk and Bjugstad 1980). In the arid conditions of the Southwest, native plants might be better adapted to climatic conditions than introduced weedy species, and might respond to herbivory by increasing their numerical abundance. The relationship that we found between levels of grazing and prairie dog burrow densities may be

the result of herbivory stimulating the growth of plants necessary to the diet of Gunnison's prairie dogs.

Our results suggest that Gunnison's prairie dogs must be conserved by maintaining habitats with a large component of native vegetation. Gunnison's prairie dogs are a natural part of native ecosystems, and have evolved alongside large herbivores such as elk, deer, and buffalo, all of which feed to some extent on native species of grasses and forbs. Native plant species have evolved to compensate for these effects of herbivory, and possibly for this reason prairie dogs might have a beneficial function of restoring rangeland that has been damaged by grazing; this is a management question that must be addressed experimentally in the future. In addition to the positive association between prairie dogs and native plant species, prairie dog towns are habitat sites that are integral to the existence of large numbers of other vertebrates and invertebrates, and eradication of prairie dogs can have detrimental consequences to natural ecosystems. Experimental and economic evidence currently indicates that eradication of prairie dogs is neither economically feasible nor particularly beneficial to cattle. We suggest that prairie dogs should be looked at in a more positive role that reflects their impact on the maintenance of natural ecosystems.

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Environmental Contaminants and the Management of Bat Populations in the United States¹

Donald R. Clark, Jr.²

Several species of bats in the U.S. form large aggregations in caves, old mines, or other shelters, and many of these colonies are of management concern to biologists working for the states or federal government (e.g. Prichard 1987). Four taxa, the gray bat (*Myotis grisescens*), Indiana bat (*M. sodalis*), Ozark big-eared bat (*Plecotus townsendii ingens*), and Virginia big-eared bat (*P. t. virginianus*), are of particular concern because they are endangered (USDI, FWS 1987).

Habitat destruction such as deforestation, water pollution, stream channelization, and stream sedimentation (Tuttle 1979, Prichard 1987) or direct human disturbance and destruction of bats (Tuttle 1979, for a recent example see Anon. 1987) are primary known threats to bat colonies. However, environmental contaminants, such as organochlorine pesticide residues and heavy metals, probably have been involved in some declines of bat populations. In this paper I discuss the management implications of these contaminants. (Note: for purposes of this discussion, "management" refers broadly to human activities undertaken in the interest of a bat colony with the goal

that colony size will remain at a steady, sustainable level or will increase to such a level.)

Examples of Possible Food-Chain Contaminant Impacts on Bat Populations

Free-Tailed Bats at Carlsbad Cavern, New Mexico

The Carlsbad population of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) was estimated at 8.7 million bats in 1936 (Allison 1937) but only 200,000 bats remained in 1973 (Altenbach et al. 1979). Several die-offs occurred during this interval (Altenbach et al. 1979), and none was linked directly to pesticide poisoning; however, routine testing of tissues was not available. The question of pesticide involvement was addressed by simulating migratory flight in young bats taken from the colony in 1974 (Geluso et al. 1976). Some of these bats died of DDE (1,1'-(dichloroethylidene)bis[4-chlorobenzene]) poisoning (DDE is the principal metabolite of DDT; 1,1'-2,2,2-(trichloroethylidene)bis[4-chlorobenzene]) due to mobilization of DDE received in their mother's milk and stored in their fat (Geluso et al. 1976). This result suggests that DDT has contributed to the decline of this population.

High DDE concentrations in the Carlsbad colony probably resulted

Abstract.—Food-chain Residues of organochlorine pesticides probably have been involved in declines of some U.S. Bat populations; examples include free-tailed bats at Carlsbad Cavern, New Mexico, and the endangered gray bat at sites in Missouri and Alabama. If a long-lived contaminant has not been dispersed in large amounts over large areas, its impact may be controlled by administrative action that stops its use or other environmental discharge, or that results in physical isolation of localized contamination so that it no longer enters food chains.

from heavy DDT use in New Mexico before its ban in 1972; however, other more-recent inputs have been postulated to explain high DDE levels in wildlife in parts of Texas, New Mexico, and Arizona (Clark and Krynit-sky 1983, Hunt et al. 1986, White and Krynit-sky 1986).

Gray Bats in Missouri

Dieldrin (3,4,5,6,9,9-hexachloro-1a,2,2a,3,6,6a,7,7a-octahydro-2,7:3,6-dimethanonaphth[2,3-b]oxirene) killed gray bats in 1976, 1977, and 1978 in two maternity colonies in Franklin County, Missouri (Clark et al. 1978b, 1983a). Residues of heptachlor-related chemicals (1,4,5,6,7,8,8-heptachloro-3a,4,7,7a-tetrahydro-4,7-methanoindene) in bats from both colonies increased to potentially dangerous concentrations in 1977 and remained elevated in 1978 (Clark et al. 1983a). Population size at one colony was estimated at 1,800 bats in 1976 and 1978, but no bats were present from 1979-82 (Clark et al. 1983a,b). Dieldrin, perhaps in conjunction with heptachlor, may have caused the decline and disappearance of this colony. Dieldrin also killed gray bats at three Boone County, Missouri, caves in 1980, 1981, and 1982 (Clark et al. 1983b, Clawson and Clark in manuscript).

Death of gray bats were attributed to dieldrin because this chemical was measured in the bats' brains at con-

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centrations known to be lethal in other species (Clark et al. 1978b). Dieldrin and heptachlor-related residues came from the use of aldrin (Dieldrin's parent compound) and, subsequently, heptachlor, to control cutworms (moth larvae, Family Noctuidae) in corn.

Gray Bats at Cave Springs Cave, Alabama

DDT was manufactured at Redstone Arsenal near Huntsville, Alabama, from 1947 to 1970, and massive amounts of DDT and its metabolites (DDD; 1,1'-(2,2-dichloroethylidene)-bis[4-chlorobenzene] and DDE) were discharged into the Tennessee River via Huntsville Spring Branch-Indian Creek (Fleming and Atkeson 1980). Local biota remains heavily contaminated (O'Shea et al. 1980, Fleming and Cromartie 1981, Fleming et al. 1984, Reich et al. 1986.).

Samples of dead or dying bats and bat guano collected between 1976 and 1986 from four gray bat colonies as far as 140 km downriver contained residues from this former discharge (Clark et al. 1988). Residues were identifiable by their high DDD to DDE ratio, which resulted from their breakdown under anaerobic conditions. Cave Springs Cave at Wheeler National Wildlife Refuge houses the colony nearest the contaminant source—about 20 km. Biologists judged that bat mortality at Cave Springs Cave was far above normal in 1978, 1985, and 1986. Residues of DDT, DDD, and DDE in brains of dead or dying bats from this cave, although elevated in comparison with residues from colonies upstream from Redstone Arsenal, were well below concentrations believed to be lethal (Clark et al. 1988). The single exception was a bat collected in 1978 with sufficient DDD in its brain (29 ppm wet weight) to have been poisoned (Clark et al. 1988). The measured residues, therefore, did not explain the observed mortalities.

Although there is no explanation for this mortality yet, another contaminant may be involved. A guano sample collected from Cave Springs Cave in 1987 was analyzed for heavy metals and cadmium measured 8.5 Ppm (dry weight). This amount may be compared with 2.2 Ppm cadmium in guano (mixed gray and southeastern bats, *M. austroriparius*) from a Florida cave where the bats were exposed to contaminations from a battery salvage plant. Kidneys of southeastern bats from this Florida cave averaged 0.89 Ppm (wet weight) cadmium with a maximum of 2.9 Ppm. Concentrations of cadmium as low as 3.4 Ppm in kidneys of voles (*Microtus pennsylvanicus*) were associated with reduced survivorship in enclosed populations. Also, six gray bats found dead in Cave Springs Cave in June 1986 were examined by the U.S. Fish and Wildlife Service's National Wildlife Health Research Center, Madison, Wisconsin. There was no evidence of injury or infectious disease, but all bats showed mild renal tubular degeneration. Because cadmium caused kidney damage (Nomiyama 1981), this metal, perhaps in combination with DDD and DDE, may have caused the recent die-off of gray bats at Cave Springs Cave. The cadmium source is unknown. Additional samples for chemical analysis will be collected in 1988.

Management of Contaminant Impacts on Bat Populations

Screening for Possible Contaminant Problems in Apparently Healthy Colonies

Contaminants that biomagnify or bioaccumulate in ecosystems include organochlorine pesticides such as DDT (and its metabolites DDE and DDD), dieldrin, heptachlor-related chemicals, and the industrial polychlorinated biphenyls (PCBs). Also included are heavy metals such as lead, cadmium, chromium, zinc, and

mercury. For chemicals that biomagnify or bioaccumulate, analyses of guano samples collected from the surface of a guano deposit can indicate body burdens in bats during their most recent activity season. Samples from greater depths may indicate contaminant concentrations in previous years.

Relationships between concentrations in guano and carcasses of bats from the same colony have been described for dieldrin, heptachlor epoxide, and DDE (Clark et al. 1982). Limited data are available on concentrations of lead, cadmium, chromium, zinc, and mercury in guano from contaminated colonies (Petit and Altenbach 1973, Clark 1979, Clark et al. 1986, this paper). About 20 grams of guano, dry weight, are necessary for analyses.

Sublethal exposure of bats to the newer organophosphorus and carbamate insecticides is demonstrated by depressed brain cholinesterase (ChE) activity in exposed individuals. Depression is determined by comparison to normal ChE activity for a sample of control bats of the same species. Measurement of ChE activity (for methods, see Ellman et al. 1961, Hill and Fleming 1982) involves removal of the brain, hence death of the bat.

Recognizing Organochlorine Pesticide-Induced Mortality in Bat Colonies

Managed colonies are usually censused annually so that any significant decline will be recognized. By also estimating numbers of dead and dying bats at these censuses, managers can differentiate between "normal" mortality and increased mortality, which may be the first sign of a contaminant problem.

May of the colonies considered most important are maternity colonies, and in maternity colonies, organochlorine chemicals kill mostly young bats. There are two reasons

for this. First, organochlorines become concentrated in the fat of mother's milk and these chemicals continually and rapidly accumulate in the young as they nurse.

For example, insects collected in foraging areas of Missouri gray bats contained a maximum of 3.1 Ppm (wet weight) dieldrin, but milk taken from the stomach of a young dead gray bat contained 89 ppm (wet weight) dieldrin (Clark and Prouty 1984). Second, young bats are 1.9 Times more sensitive than adults to dieldrin and 1.5 Times more sensitive to DDT (Clark et al. 1978a, 1983a). Young bats dying of organochlorine poisoning may still have milk in their stomachs unlike young dying of starvation. Therefore, increased infant mortality in a maternity colony with some young having milk in their stomachs may indicate poisoning by an organochlorine chemical.

Diagnosing Chemical Poisoning in Bats

Diagnosis for organochlorine chemicals requires analyses of brains and interpretation of the resulting measurements. However, because concentrations in brains are closely correlated with concentrations in carcass fat (Clark 1981a), analyses of carcasses may serve if brains are unavailable. For example, analysis of carcasses may be the only option when bats are partly decomposed. Correlations between brain and carcass fat concentrations only have been quantified for DDE, DDT, and dieldrin (Clark 1981a).

Lethal brain concentrations for DDE, DDT, dieldrin, and PCB (Aroclor 1260) have been determined for at least one species of bat (Clark 1981b). Because lethal brain levels are fairly similar among mammals and birds, comparisons can provide clues about the effect on a populations, even though the lethal level for the species under investigation has not been determined yet.

Diagnosis of death in bats from heavy-metal poisoning is less certain, but interpretations often can be made based on other species of mammals (Clark 1979, this paper). Diagnosis for heavy metals involves analyzing liver and kidneys along with histological examination for damage.

Death in bats caused by the anticholinesterase insecticides could be diagnosed by measurement of depressed brain ChE in combination with detection of an anticholinesterase chemical in the contents of the gastrointestinal tracts or other tissues of the affected bats. Lethal depression of brain ChE has been measured in little brown bats (*M. lucifugus*) in the laboratory for methyl parathion (phosphorothioic acid *O,O*-dimethyl *O*-(4-nitrophenyl)ester) and Orthene® (acephate; acetylphosphor-amidothioic acid *O,S*-dimethyl ester) (Clark 1986, Clark and Rattner 1987).

Even though a firm diagnosis of contaminant-induced mortality requires tissue analyses, analysis of a guano sample, as a first step, may indicate whether organochlorines or metals are involved.

Chemical analyses of tissues or guano are not something that managers usually can perform themselves. However, an Environmental Contaminant Field Specialist from the U.S. Fish and Wildlife Service can be contacted (there are 1-3 in each state); if he or she determines that the situation warrants, analyses can be done. The Specialist also may send specimens to the National Wildlife Health Research Center if disease is suspected.

Bat specimens for diagnostic study generally should be frozen immediately. However, examinations for diseases and histopathology require that specimens be kept refrigerated but not frozen until organs can be removed and preserved in fluid. Control specimens of the same species are necessary for diagnosis of depressed brain ChE activity. Guano does not require freezing or refrigeration. The Contaminant Field Spe-

cialist can provide detailed instructions for specimen collection and handling.

Possible Impacts of New Generation Pesticides on Bat Colonies

Most organochlorine pesticides have been banned or their use otherwise reduced in the U.S., And some wildlife-related problems have improved. Organochlorines largely have been replaced by organophosphorus (e.g., Acephate, diazinon [phosphorothioic acid *O,O*-diethyl *O*-[6-methyl-2-(1-methylethyl)-4-pyrimidinyl]ester], and methyl parathion) and carbamate (e.g., Aldicarb [2-methyl-2-(methylthio)propanal *O*-[(methylamino)carbonyl]oxime], carbaryl [1-naphthalenol methylcarbamate], and carbofuran [2,3-dihydro-2,2-dimethyl-7-benzofuranol methylcarbamate]) insecticides. These chemicals are relatively short-lived and generally do not accumulate in food chains. Exposure in bats probably occurs when they feed over fields or orchards that are being, or have just been, sprayed. In these cases, bats might be sprayed directly and receive the chemical through their skin and lungs. Pesticides are frequently sprayed in the evening, at night, or early in the morning to avoid killing honey bees, to kill adult mosquitoes, or to take advantage of quiet wind conditions and thereby avoid drift. Bats also may be exposed by eating insects that have just been sprayed but are still alive.

New-generation pesticides have not yet been linked to bat die-offs, but, in 1968, ranchers and farmers in a cotton-growing area of Arizona reported "...unusual Numbers of dead or dying (free-tailed) bats in their fields...Many Were found convulsing, incapable of flight" (Reidinger and Cockrum 1978). This mortality was attributed to DDT; however, chemical analyses indicated that neither lethal residues of DDT nor its

metabolites had been present in these bats (Clark 1981b). Because methyl parathion also was commonly used on cotton in this region, mortality may have been caused by this organophosphorus pesticide. The mortality pattern described by ranchers and farmers where bats were scattered on the ground in an incapacitated condition suggests quick intoxication after direct contact with a chemical of high acute toxicity such as the organophosphate methyl parathion (see Clark 1986).

Reducing Contaminant Impacts in Bat Colonies

What can be done once it is determined that bats have died from a food-chain contaminant? The answer will depend on the contaminant, its source, and on the ability or authority of the manager to change local practices or obtain cleanup procedures.

When large quantities of a long-lived chemical have been incorporated into soils over vast areas, such as DDE in New Mexico or dieldrin in Missouri, the chemical will continue to enter food chains for many years. The manager of an affected bat colony can only protect the colony from other sources of damage and hope that it survives until the contamination dissipates. If the colony is extirpated, the manager can protect the site so that it might be recolonized from outside the contaminated area in the future.

After a colony is known to be heavily contaminated with an organochlorine or metal, annual analyses of guano can determine whether contamination is decreasing, increasing, or remaining stable, and also can alert the manager to potential problems. For example, in Missouri, heptachlor epoxide increased from minor amounts in bats in 1976 to near lethal levels in 1977 (Clark et al. 1983a). Such information promptly passed to the state authorities might

persuade them to recommend a different pesticide to farmers before the problem chemical becomes heavily dispersed over wide areas.

The Alabama example given previously shows that large cleanup efforts are possible if the contamination is, in total or in part, localized. State and federal agencies represent routes open to managers. In this instance, the U.S. Environmental Protection Agency exercised its authority. Whether a large cleanup effort would be undertaken if only bats were affected is not known; however, if organochlorine contamination is heavy enough to cause mortality in bat colonies, it probably affects other wildlife as well. Bat colonies are good places to look for food-chain contaminant problems because bats feed over wide areas but congregate in only a few roosts. Thus, problems from many potential areas are brought to a single site where symptoms may be seen as dead or dying bats. The disadvantage is that it may be difficult to locate the source area, or areas, unless the feeding locations of the bats are known.

Heavy metals in the environment often have industrial point sources that are subject to existing emission regulations. Therefore, such contamination may be easier to stop.

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Habitat Structure, Forest Composition and Landscape Dimensions as Components of Habitat Suitability for the Delmarva Fox Squirrel¹

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The Delmarva fox squirrel (*Sciurus niger cinereus*) was placed on the federal endangered species list in 1967 (32 FR 4001; U.S. Department of Interior 1970). Remnant populations were restricted to four counties in eastern Maryland (Taylor and Flyger 1973), representing less than 10% of the historic range of the subspecies on the Delmarva Peninsula. Forest clearing and habitat fragmentation throughout the range undoubtedly contributed significantly to the present endangerment (Taylor 1973).

The U.S. Fish and Wildlife Service Recovery Plan for the restoration of the Delmarva fox squirrel to secure status emphasizes both the reintroduction of this subspecies to suitable habitats throughout the former range and prescriptive habitat management for established populations (Taylor et al. 1983). A thorough understanding

of habitat requirements will be essential for both initiatives (Dueser and Terwilliger 1988).

Habitat requirements might be expressed through any of three separate but related components of habitat suitability: forest habitat structure, forest tree species composition, and surrounding landscape structure. Both habitat structure and forest composition have been shown to influence the distribution and abundance of fox squirrels in heterogeneous landscapes (Nixon and Hansen 1987).

Recent research has demonstrated the potential influence of landscape composition and structure on populations of woodland mammals occupying farmland mosaics (Wegner and Merriam 1979, Middleton and Merriam 1983, Fahrig and Merriam 1985). Furthermore, changes in the landscape of the Delmarva Peninsula almost certainly played a major role on the decline of the fox squirrel (Taylor 1973).

Given this background, the objective of this study was to compare the apparent effects of habitat structure, forest composition and landscape dimensions on the presence and absence of the Delmarva fox squirrel on 54 study sites in eastern Maryland. This analysis is the first step in the development of a predictive classification model of habitat suitability for this subspecies (cf. Houston et al. 1986).

Abstract.—Discriminant function analysis comparing 36 occupied and 18 unoccupied sites revealed that structural variables discriminated between sample groups better than compositional variables, and the latter discriminated better than landscape variables. These results are encouraging that habitat structure will provide a reliable basis for a predictive classification model of habitat suitability. Such a model would be useful both for pre-screening the biological suitability of potential release sites and for planning, implementing and monitoring prescriptive habitat management.

Methods

Data Base

During a 12-mo search for remnant populations of the Delmarva fox squirrel on the Maryland Eastern Shore, Taylor (1976) located 36 "fox squirrel present" (Present) sites with extant populations and 18 "fox squirrel absent" (Absent) sites. The gray squirrel (*Sciurus carolinensis*) was present on all 54 sites. Taylor then sampled the forest habitat of each site, to compare Present forest stands with Absent stands. He established a representative 4 m x 200 m belt transect on each site, on which he recorded the number of trees by species per diameter-breast-height (DBH) size class (5-20 cm, 20.1-30 cm, 30.1-50 cm, and 50.1+ cm), percent crown cover, percent understory cover, understory density, and understory species composition. All habitat measurements were taken from June through September 1972 and 1973. These data formed the initial data base for this study.

Taylor (1976) reported the number of trees measured in each of two size classes: "small" trees (5-30 cm DBH) and "large" trees (> 30 cm DBH). We assigned each tree to one of five taxonomic groups: loblolly pine (*Pinus taeda*), combined oak species (*Quercus* spp.), American beech (*Fagus grandifolia*), combined hickory species (*Carya* spp.), and combined mixed

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hardwoods. We estimated the approximate total basal area for each size-taxonomic class by assuming an average DBH of 17.5 cm for small trees and 40.0 cm for large trees. We then estimated total basal area for all trees ≥ 5 cm DBH and the fraction of that total basal area represented by each taxonomic group. These basal area estimates provide a basis for comparing forest "composition" independently of forest "structure" as reflected, for example, in the raw percentage of trees counted in each taxonomic group.

Original data were collected on land use and cover composition of the landscape surrounding a random subset of Taylor's (1976) study areas (fig. 1). Landscape variables included area of open fields, percentage of area forested, internal forest perimeter ("edge") within the sample unit, forest shape (Blouin and Connor 1985), and distance to next nearest woodland. These variables are referred to below as landscape "dimensions." They were measured by

planimetry of 1:1000 black-and-white photographs (dated 1978) obtained from Eastern Shore offices of the USDA Agricultural Stabilization and Conservation Service. We initially measured each landscape variable for a 2-km² circular sample unit centered on the sample woodland. This unit was chosen as a first-approximation of "minimal population area" on the basis of home range size and activity (Flyger and Smith 1980). Based on the results of analyses for the 2-km² unit, both smaller (1-km²) and larger (4-km²) sample units subsequently were described in the same way.

Statistical Analyses

This comparison of habitat components is based on multivariate statistical analyses of three separate but related components of forest habitat suitability: (1) habitat structure ("What does the forest 'look like' to an observer passing through on the

ground?"), (2) tree species composition ("Which tree species predominate in this forest and give it its character?"), and (3) landscape dimensions ("What are the land use and cover dimensions of the landscape mosaic in which this forest is embedded?"). Conceptually, these components represent a gradient of scales from "microscopic" habitat structure to "macroscopic" composition to "megascopic" context.

Two-group discriminant function analysis was used to compare the Present and Absent forest stands identified by Taylor (1976). Each analysis (1) computed the univariate F-ratio comparing Present and Absent sites for each habitat variable, (2) tested the centroids of Present and Absent sites for equality on the basis of a linear combination of the habitat variables (i.e., a linear discriminant function), using multivariate analysis of variance (MANOVA), (3) indicated the relative contribution of each habitat variable to any observed difference between centroids, based on the correlation between the variable and the discriminant function, (4) tested the sample variance-covariance matrices of Present and Absent sites for homogeneity using a Box's M test statistic, and (5) indicated the percentage of the variation in group membership (Present or Absent) explained by the discriminant function, based on the correlation between the membership variable and the discriminant function. (Dueser and Shugart 1978). All analyses were computed both with and without arcsin-square root transformations of percentage variables. Results of the parallel analyses were qualitatively similar in each case. For purposes of interpretability, only the results for untransformed variables are presented here. All analyses used the MANOVA and DISCRIMINANT routines of the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975).

As an unbiased test of the ability of each set of habitat variables to

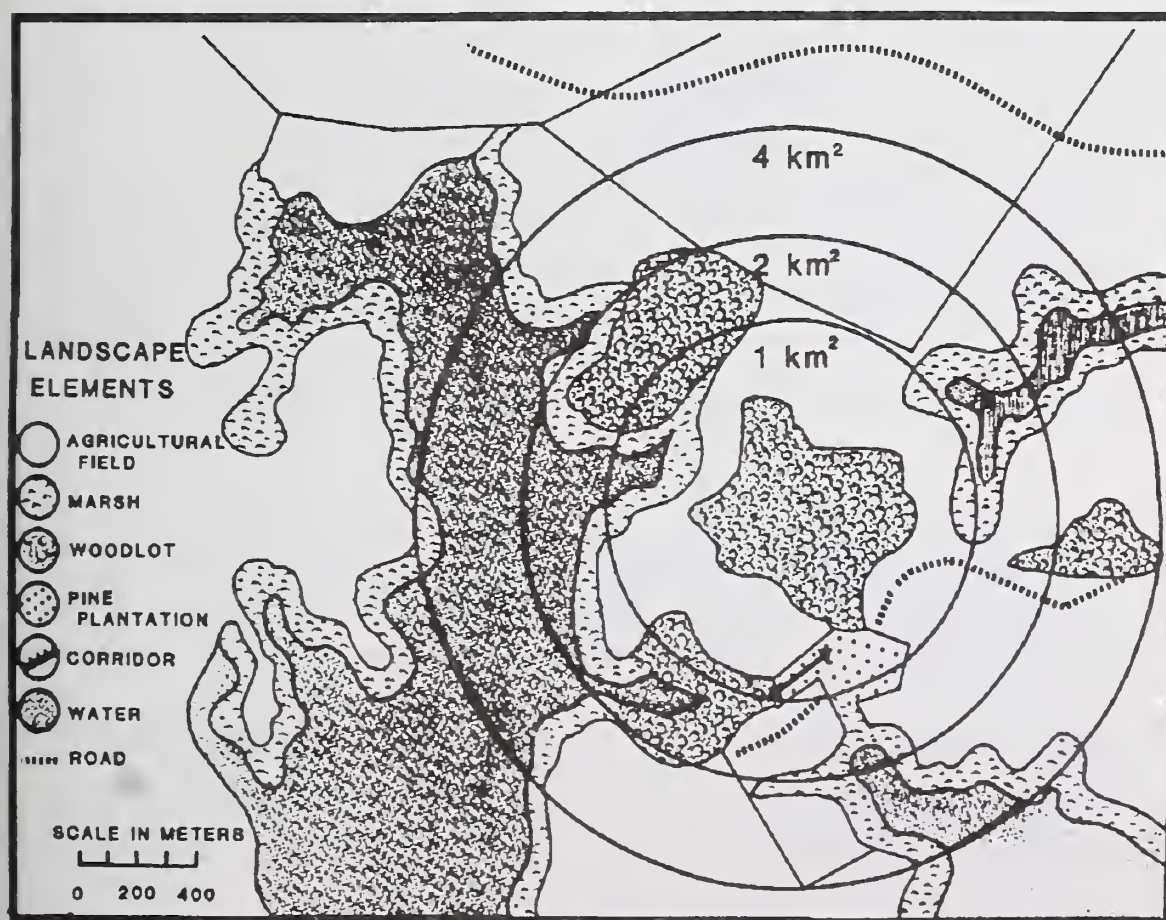


Figure 1.—Schematic diagram of 1-, 2- and 4-km² sample units for measuring landscape dimensions of "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland. Each sample unit was centered on one of Taylor's (1976) study areas.

classify the group membership of the study sites (i.e., Present or Absent), a jackknife procedure (Efron 1979) was used to classify each of Taylor's study areas. Each site was deleted in sequence, DISCRIMINANT was run for data from the remaining 53 sites, and a classification function was computed from these data. The deleted site was then classified on the basis of this independent classification function. The probabilistic ("predicted") classification was then compared with the actual ("observed") classification for each site.

Brennan et al. (1986) have proposed an alternative solution to the problem of habitat analysis. Logistic regression analysis is superior to multivariate analysis of variance when one or more of the predictor (e.g., habitat) variables is categorical (i.e., non-continuous), when the variance-covariance matrices are non-homogeneous and/or when the data violate the assumption of multivariate normality (Press and Wilson 1978). Parallel analyses demonstrate that logistic regression analysis offers no inherent advantage over discriminant function analysis in the present case (Dooley, unpublished).

Results

Habitat Structure

Present sites had a greater percentage of trees larger than 30 cm DBH, lower percentage shrub-ground cover, and slightly lower understory vegetation density than Absent sites (table 1, $p \leq 0.05$). Present and Absent sites differ structurally on the average (MANOVA Chi-square (5) = 14.825, $p \leq 0.011$). The linear combination of structure variables accounted for 26% of the variation in group membership. The variance-covariance matrices were marginally homogeneous (Box's M = 20.056, $p \geq 0.06$). Percentage of trees greater than 30 cm DBH ($r = -0.735$), understory vegetation density (0.564), and per-

centage shrub-ground cover (0.564) are particularly important in discriminating between sites. Conceptually, Present sites have larger trees, less shrub-ground cover vegetation, and less understory than Absent sites (fig. 2). Present sites were correctly classified 79% of the time in the jackknifing procedure, and Absent sites were correctly classified 48% of the time.

Forest Tree Species Composition

All 54 study areas supported a mix of hard- and soft-mast tree species. Although Present sites had somewhat greater basal areas for American beech ($p > 0.07$) and mixed hardwoods ($p > 0.05$), there were no clear-cut univariate differences between sites in forest composition (table 2). There also was no difference in total

Table 1.—Comparison of average forest habitat structure for "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland, based on data of Taylor (1976). Tabled values are means and (standard deviations).

Habitat variables	Present (N = 36)		Absent (N = 18)		P
% Trees > 30 cm DBH	32.3	(12.14)	22.1	(9.26)	<0.01
% Crown cover	75.6	(17.72)	70.6	(16.08)	>0.30
% Shrub-ground cover	51.1	(26.60)	67.5	(21.85)	<0.05
Understory "density"	2.6	(1.38)	3.4	(1.04)	<0.05
% Pine composition	10.5	(10.63)	17.1	(22.23)	>0.10

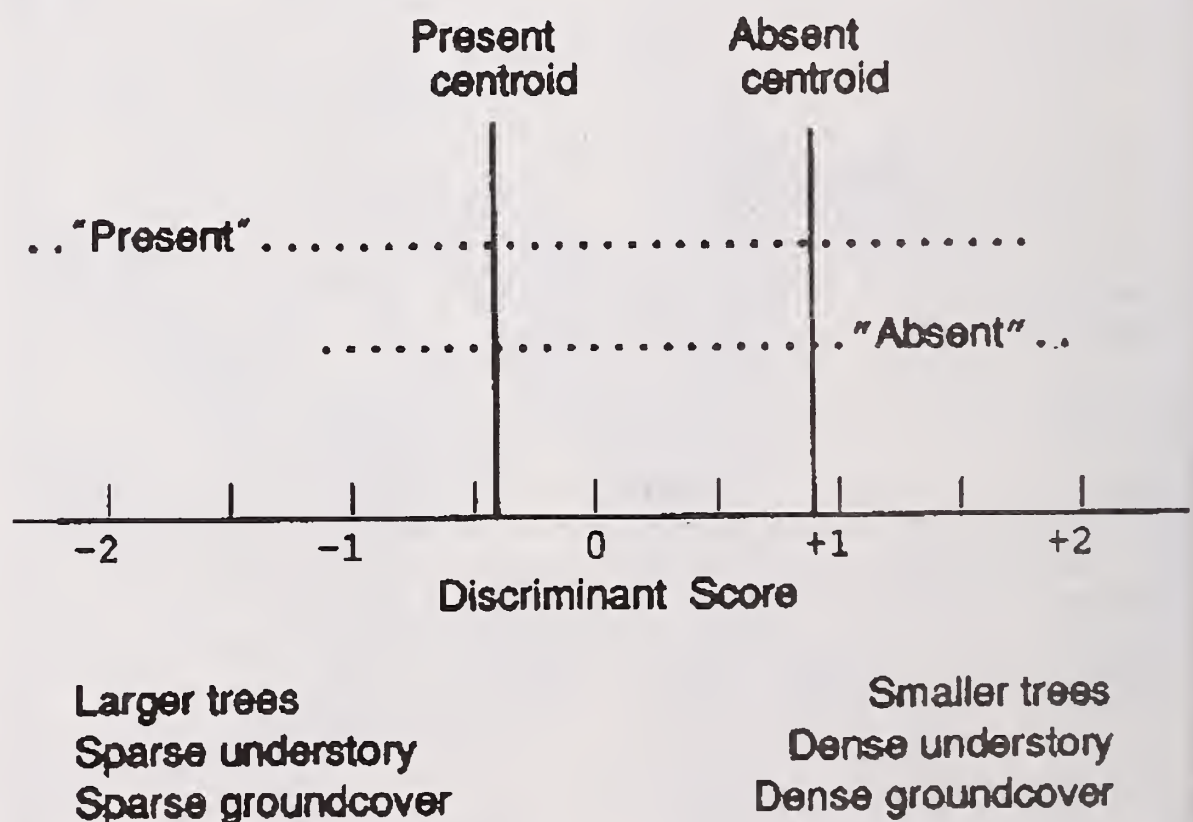


Figure 2.—Interpretation of discrimination between average "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland, based on analysis of forest habitat structure. The horizontal dashed lines indicate the range of observations for a sample group (Present or Absent).

basal area ($F(1,52) = 2.300, p > 0.13$). The two types of sites were similar in composition for both small and large trees (fig. 3). Reflecting this similarity, there was only a marginally significant multivariate difference in forest composition (MANOVA Chi-square (5) = 10.584, $p > 0.06$).

The linear combination of composition variables accounted for 19% of the variation in group membership. The variance-covariance matrices were conspicuously non-homogeneous (Box's $M = 61.549, p < 0.001$). Present sites were correctly classified 79% of the time, and Absent sites were correctly classified 48% of the time.

Although the correct classification rates were the same as for structural variables, the two sets of variables misclassified different sites.

Landscape Dimensions

Five landscape variables were measured for the 2-km² circular sample unit centered on the target woodland of 38 of the Taylor's (1976) study areas. Present sites were somewhat closer to the next nearest forest tract than Absent sites (table 3, $p < 0.03$). Despite this modest difference, there was no significant multivariate difference in landscape dimensions between sites (MANOVA Chi-square (5) = 8.574, $p > 0.127$).

Present and Absent woodlands also were similar in area, averaging 9.4 and 10.0 ha, respectively, as photographed in 1978. The linear combination of landscape variables accounted for 23% of the variation in group membership. The variance-covariance matrices were homogene-

ous (Box's $M = 19.926, p > 0.39$). As with forest composition, there was no consistent difference in landscape dimensions between Present and Absent sites. Present sites were correctly classified 78% of the time, and Absent sites were correctly classified 40% of the time.

To evaluate the possibility that the negative result in the test for equality of group centroids came about because we were measuring landscape variables on an "incorrect" spatial scale, we repeated the landscape analysis for both smaller (1-km²) and larger (4-km²) circular sample units, still centered on the woodland of interest. Again, there were no consistent group differences on either scale ($p > 0.40$, table 4).

Either the landscapes surrounding the sample Present and Absent woodlands do not differ consistently, or they differ on a scale of measurement or in a way not revealed by the present analyses.

Table 2.—Comparison of average tree species composition for "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland, based on estimated basal area (cm² per 800-m² sample transect) per taxonomic group. Data from Taylor (1976). Tabled values are means and (standard deviations).

Taxonomic group	Present (N = 36)		Absent (N = 18)		P
Loblolly pine	5359	(1099.84)	7339	(2278.43)	>0.35
Oak species	9547	(1061.24)	9628	(1378.18)	>0.95
American beech	3293	(679.62)	1400	(546.56)	>0.07
Hickory	1583	(611.77)	1050	(263.26)	>0.50
Mixed hardwoods	9498	(1032.96)	6514	(690.13)	>0.05

Table 3.—Comparison of average landscape dimensions for "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland. Variables measured for 2-km² circular sample unit centered on study woodland. Tabled values are means and (standard deviations).

Landscape variables	Present (N = 27)		Absent (N = 11)		P
Area open fields (ha)	99.3	(6.4)	96.3	(11.9)	>0.81
% Forested area	56.4	(3.6)	50.1	(6.0)	>0.35
Internal perim. (km)	5.3	(2.0)	6.2	(1.9)	>0.21
Forest "shape"	136.4	(54.5)	153.0	(44.9)	>0.38
Dist. next woodlot (km)	0.4	(0.1)	0.8	(0.2)	<0.03

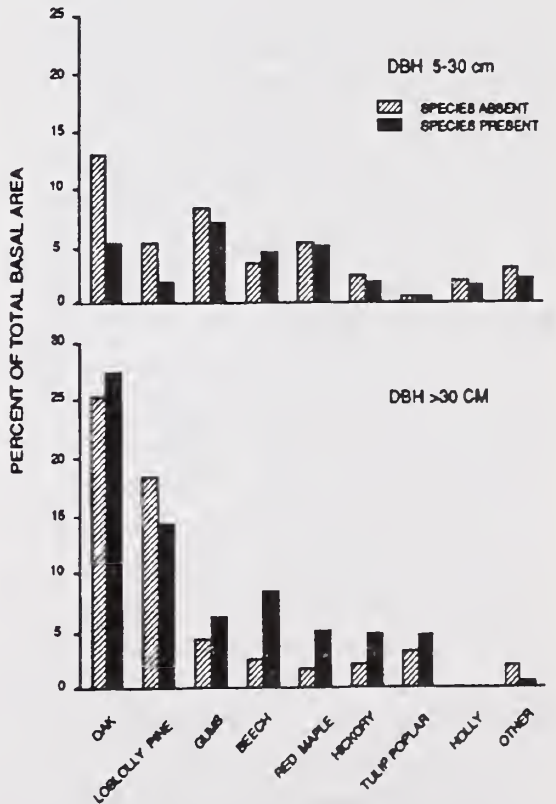


Figure 3.—Average forest tree species composition of "fox squirrel present" and "fox squirrel absent" study areas on the Eastern Shore of Maryland. "Other" category includes a variety of small trees such as cherry (*Prunus* spp.) and flowering dogwood (*Cornus florida*).

Discussion

Present Habitat

The present habitat of the Delmarva fox squirrel consists primarily of relatively small stands of mature mixed hardwoods and pines having relatively closed canopies, relatively open understory, and a high proportion of forest edge. Occupied tracts include both groves of trees along streams and bays and small woodlots located near agricultural fields. In some areas, particularly in southern Dorchester County, Maryland, occupied habitat includes tracts dominated by mature loblolly pine located adjacent to marshes and tidal streams. The woodland habitats now occupied by the Delmarva fox squirrel are consistent with those occupied by other subspecies of fox squirrel (Bakken 1952; Brown and Yeager 1945; Weigl et al., in press).

The picture of the Delmarva fox squirrel that emerges from the literature is one of a species relatively adept at utilizing a dissected, heterogeneous landscape dominated by agriculture and woodlot forestry. Fox squirrels are more cursorial than gray squirrels, and often are found on the ground several hundred meters from the nearest woodlot. They occupy larger home ranges than gray squirrels (30 ha vs. 3 ha), travel farther between captures (307 m vs. 119 m), and thus are generally more mobile (Flyger and Smith 1980). Fox squirrels more readily exploit agricultural crops such corn, oats, soybeans and fruit. They more frequently utilize forest edges. Fox squirrels would thus appear to be relatively well-adapted to exploit the landscape created by settlement of the coastal plain.

One might conclude that man's activities on the Delmarva Peninsula should have been to the benefit of the fox squirrel. Land clearing has created woodlots. Grazing and burning have opened up the understory. Agriculture has increased the availabil-

ity of alternative food sources and perhaps stabilized the food supply. Indeed, Allen (1943) and Nixon and Hansen (1987) indicate that settlement and agriculture have worked to the advantage of the fox squirrel throughout the midwestern United States, resulting in increased abundance and an expanded geographic range.

Why has this not occurred with the Delmarva subspecies? Why has the abundance of this fox squirrel continued to decline throughout the period of the recorded literature (since approximately 1850)?

Taylor (1976) attributes the continued decline of the Delmarva fox squirrel to habitat destruction. While many of the landscape changes resulting from settlement might have benefited the fox squirrel, others have been detrimental. Taylor believes that extensive timber harvest has been particularly detrimental. The removal of mature hardwoods has reduced the availability of suitable den trees, removed reliable sources of concentrated hard mast, promoted the luxuriant growth of understory vegetation, and perhaps altered the competitive relationship between fox and gray squirrels to favor grays. Furthermore, coastal plain woodland management typically has involved both short timber rotations (i.e., frequent harvests) and reforestation with pure stands of loblolly pine. Finally, gradual urbanization has added yet another detrimental land-use practice.

Habitat Suitability

It is assumed that Present (i.e., occupied) sites are more "suitable" on the average than are Absent (i.e., unoccupied) sites. Present sites are regarded here as the "standard of excellence" by which to judge the habitat requirements of the Delmarva fox squirrel. Given that a number of unknown (and unknowable) ecological, biogeographical, and/or historical factors may actually be responsible for the absence of this subspecies from any particular site within the historic range, this assumption is correct only as a first approximation (ref. Hanski 1982). It clearly would be unwarranted if the distribution of squirrels among these 54 study sites were highly variable through time. Nevertheless, the chance presence of the squirrel on "unsuitable" sites and its absence from "suitable" sites because of factors other than habitat suitability per se can only make it more difficult to distinguish between Present and Absent sites. These analyses based on presence-or-absence population information thus circumvent many of the potential pitfalls associated with the use of population density as an indicator of habitat suitability (Van Horne 1983).

Given its present habitat, it seemed reasonable to propose that the capacity of a woodland to support a population of the Delmarva fox squirrel could be determined by habitat structure, forest composition and/or the land use and cover com-

Table 4.—Comparison of average "fox squirrel present" and "fox squirrel absent" study areas at the 1-, 2- and 4-square kilometer scales of observation. Testing for similarity of landscape dimensions listed in table 3.

Statistic	1-km ²	2-km ²	4-km ²
Number "Present" areas	7	27	7
Number "Absent" areas	9	11	9
Chi-square	4.791	8.574	2.750
df	5	5	5
p	0.442	0.127	0.738

position of the surrounding landscape. We anticipated originally that each of these components of habitat suitability would prove to be important in its own way, and that each would have a perceptible influence on fox squirrel presence or absence in Maryland woodlots today. Our results indicate, however, that habitat structure is the component most likely to contribute meaningfully to the formulation of a predictive model of habitat suitability. Only the structure variables discriminate strongly between Present and Absent sites: Present sites have larger trees, less ground cover and less understory (fig. 2). These variables account for the greatest fraction of the explained variation, their dispersion matrices are effectively homogeneous, and they classify sites to the correct group (i.e., Present or Absent) at least as well as any of the variable sets examined.

Forest composition is highly variable among locations in eastern Maryland, but this variation seems to exert only a marginal influence on the likelihood of occurrence of fox squirrels on any given site. The composition variables classify sites as reliably as the structural variables, and they account for only a slightly lower fraction of the explained variation. They do not, however, discriminate strongly between Present and Absent sites and their dispersion matrices are strongly non-homogeneous. Of course, this conclusion is based on a comparison of two groups of sites, all of which are known to be "squirrel woods." Had there been a "tree squirrel absent" category of study area, forest composition might well have appeared to be more significant (cf. Nixon et al. 1978, Sanderson et al. 1976).

Landscape composition also varies among locations, but this variation seems not to be important on the average in discriminating between occupied and unoccupied sites today. The landscape variables account for a comparable fraction of the explained

variation, they classify sites almost as reliably as the structural variables, and their dispersion matrices are homogeneous. They do not, however, discriminate meaningfully between Present and Absent sites. Given the suggested importance of landscape changes in bringing about the decline of the fox squirrel, this result was somewhat unexpected. The correct interpretation probably requires recognition that most of the Eastern Shore landscape has been altered, fragmented and homogenized. Most of the remaining woodlands are mere remnants of forest in a mosaic of agricultural fields, wetlands and suburban development. There may simply be little important variation remaining among these forest patches. At the same time, it must be recognized that a number of potentially important landscape variables—e.g., proximity to streams and ponds (McComb and Noble 1981) and proximity to roadways (Flyger and Lustig 1976)—were not considered in this analysis.

Management Implications

The Recovery Plan for the Delmarva fox squirrel calls for both the translocation of squirrels to suitable habitats throughout the historic range and the maintenance of occupied habitat (Taylor et al. 1983). Will objective, quantitative habitat analysis be helpful in evaluating potential release sites and planning prescriptive habitat management? Results of the analyses presented here provide some basis for optimism. A number of management implications follow from these results:

1. Of the variable sets examined, habitat structure is the best indicator of biological habitat suitability for the Delmarva fox squirrel at the present time. Even this minimal list of structure variables (table 1) has the power to

discriminate meaningfully between occupied and unoccupied forest stands. Present sites have larger trees, less ground cover, and less understory than Absent sites. Significantly, these results corroborate the general habitat descriptions reported by Flyger and Lustig (1976).

2. In addition to this clear-cut discrimination, the structure variables exhibit the most desirable combination of statistical properties, including the highest variance explanation, homogeneity of dispersions, and high correct classification rates. These properties will simplify the formulation of a predictive classification model of habitat suitability.
3. Although the absence of meaningful discriminating information in forest composition and landscape dimensions was somewhat surprising, these results have the effect of simplifying the effort to quantify habitat suitability for the Delmarva fox squirrel. It would be imprudent to disregard forest composition and landscape attributes in the evaluation of potential release sites; these components of habitat suitability must be important at some level (Flyger and Lustig 1976). There appears to be little potential, however, for the variables analyzed here to contribute to a predictive model of habitat suitability.
4. The discriminating structure variables are easy and relatively inexpensive to measure. Including site reconnaissance, approximately one-half day of field time is required for a team of two ex-

perienced observers to collect a Taylor-type data set.

5. It should therefore be practical to pre-screen potential release sites for habitat suitability relative to Present sites. Objective pre-screening has not always been possible because no "standard of excellence" has been available.
6. It also should be practical to plan, implement and evaluate prescriptive habitat management for the benefit of the Delmarva fox squirrel on occupied sites or potential release sites. The important measures of habitat structure (e.g., understory vegetation density) tend to be variables which are amenable to silvicultural manipulation (Nixon et al. 1980).

Conclusions

We anticipated at the outset that each of three potentially important components of habitat suitability—forest habitat structure, forest tree species composition, and surrounding landscape dimensions—would influence the present occurrence of the Delmarva fox squirrel in forest stands on the Eastern Shore of Maryland. The analyses reported here produced a number of surprises.

Habitat structure is the only component that both discriminates between occupied and unoccupied sites in a meaningful way and exhibits a combination of statistical properties favorable for the formulation of a predictive classification model of habitat suitability.

The analysis of habitat structure provides a basis for optimism that such a model would prove useful both for pre-screening potential release sites and for planning, implementing and monitoring prescriptive habitat management.

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Effects of Treating Creosotebush With Tebuthiuron on Rodents¹

William G. Standley² and Norman S. Smith³

Herbicides are often used to control shrubs such as mesquite (*Prosopis juliflora*) and creosotebush (*Larrea tridentata*), which have invaded millions of hectares of semidesert grasslands (Cox et al. 1982). The reduction of shrub cover usually results in an increase in forage production (Box 1964).

The herbicide 2,4-D has been used for more than two decades and its effects on rodent communities have been extensively studied (Keith et al. 1959, Johnson and Hansen 1969, Spencer and Barrett 1980). 2,4-D has varied effects on rodent communities, increasing the abundance of some species, while decreasing the abundance of others (Johnson and Hansen 1969, Spencer and Barrett 1980).

Tebuthiuron is a thiadiazolyl-urea herbicide (Walker et al. 1973) used to control shrubs in the southwest (Herbel et al. 1985). No studies have been conducted to determine effects of tebuthiuron treatments on rodent

communities. We studied grasslands invaded by creosotebush in southeastern Arizona in order to determine changes that take place in a rodent community due to treatment with tebuthiuron. We compared vegetation and nocturnal rodents present on control and treated plots. Because tebuthiuron is nontoxic to laboratory mice, rats, and rabbits (Morton and Hoffman 1976) we assumed that any changes in the rodent community would be in response to

changes in food supply, ground cover, or both.

Methods

Two adjacent 150 x 600 m plots were fenced from cattle, and one was aerially treated with tebuthiuron (1.0 kg/ha) in May 1981 as part of an ongoing experiment on the USDA Forest Service Santa Rita Experimental Range, 45 km south of Tucson Ari-

Table 1.—Mean (%) vegetative cover on tebuthiuron treated and control plots (N=6).

Species	Treated		Control	
	X	SE	X	SE
Grasses				
Threeawn (<i>Aristida</i> sp.)	18.5	3.2	0.1	0.1
Bush muhly (<i>Muhlenbergia porteri</i>)	10.0	2.5	11.0	3.4
Fluffgrass (<i>Tridens pulchellus</i>)	3.0	1.3	0.7	0.7
Other	0.3	0.3	0.0	0.0
Total	31.8	1.9	11.8	3.2
Shrubs				
Creosotebush (<i>Larrea tridentata</i>)	0.2	0.1	33.9	4.6
Mesquite (<i>Prosopis juliflora</i>)	0.0	0.0	1.4	0.9
Desert zinnia (<i>Zinnia pumila</i>)	0.0	0.0	3.3	1.4
Desertbroom (<i>Baccharis sarothroides</i>)	0.5	0.5	0.0	0.0
Total	0.7	0.5	38.6	4.5

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zona. Vegetation on the plots is dominated by creosotebush, with sparse grasses such as threeawn (*Aristida* sp.) and bush muhly (*Muhlenbergia porteri*) (Martin and Reynolds 1973).

We sampled vegetation and rodent communities in June 1984, three years after herbicide treatment. Vegetation was sampled using the line intercept method (Canfield 1941). Six 30 m parallel lines were systematically located on each plot. Total intercepts of each species were averaged and transformed into percent ground and canopy cover. Rodent communities were surveyed using the removal method. Sherman live-traps (7.5 x 7.5 x 25 cm) were used so that rodents could be used for other studies. Three 8 by 8 grids with traps spaced at 10 m intervals, were placed on each plot. Grids were placed as far from each other and from plot boundaries as possible, resulting in a uniform distribution. Traps, opened at sunset and closed at

sunrise, were baited with peanut butter and oats. We prebaited traps for one night then removed all rodents captured during the following four nights. The total number of each species captured on the three grids on each plot were averaged.

Results

Average grass cover on the tebuthiuron-treated plot was almost three times that on the control plot (table 1), with threeawn contributing most of the difference. Average shrub cover on the treated plot was 98% lower than on the control plot, with creosotebush accounting for the biggest difference.

On tebuthiuron-treated grids we captured 162 rodents of eight species, and on control grids 95 rodents of eight species (table 2). Higher numbers of Arizona cotton rats (*Sigmodon arizonae*) and western harvest mice (*Reithrodontomys megalotis*) on the

treated grids accounted for most of the difference in abundance. Cotton rats and house mice (*Mus musculus*) were captured only on the treated grids, while Bailey's pocket mice (*Perognathus baileyi*) and deer mice (*Peromyscus maniculatus*) were caught only on control grids.

Discussion

The dramatically greater grass cover and lesser shrub cover on the treated plot are consistent with results of other experiments with tebuthiuron (Herbel et al. 1985), as well as with 2,4-D (Spencer and Barrett 1980). This difference in vegetative structure appears to account for most of the differences in the rodent community. Studies of cotton rats and harvest mice have shown that both species are strongly associated with dense stands of grass (Goertz 1964, Ford 1977). The similarity in abundance of Merriam's kangaroo rats on control and treated plots was unexpected since heteromyids are generally more abundant in areas with sparse ground cover (Stamp and Ohmart 1978).

We do not present inferential statistics to test differences in ground cover or rodent numbers because both the line intercept transects and trap grids were actually subsamples rather than true replicates (Hurlbert 1984). We are convinced, however, that differences between plots in numbers of cotton rats and harvest mice, are the result of habitat changes following treatment with tebuthiuron.

Because of the low numbers of deer mice and Bailey's pocket mice captured on the control plots, we do not feel their absence on the treated plots is significant. Because the responses were either neutral or positive, we feel that tebuthiuron can be safely used by managers to control shrubs in semidesert grasslands without fear of endangering rodents directly. However, the impact of

Table 2.—Mean number of rodents captured on tebuthiuron treated and control plots (N=3).

Species	Treated		Control	
	X	SE	X	SE
Merriam's kangaroo rat (<i>Dipodomys merriami</i>)	15.7	4.3	13.0	2.1
Arizona pocket mouse (<i>Perognathus amplus</i>)	5.3	2.6	7.0	0.6
White-throated wood rat (<i>Neotoma albigula</i>)	8.0	1.5	4.3	1.5
Western harvest mouse (<i>Reithrodontomys megalotis</i>)	10.0	1.5	0.3	0.3
Arizona cotton rat (<i>Sigmodon arizonae</i>)	8.0	3.2	0.0	0.0
Desert pocket mouse (<i>Perognathus penicillatus</i>)	3.0	0.0	4.0	1.0
Southern grasshopper mouse (<i>Onychomys torridus</i>)	3.7	0.3	1.7	0.7
Bailey's pocket mouse (<i>Perognathus baileyi</i>)	0.0	0.0	1.0	1.0
Deer mouse (<i>Peromyscus maniculatus</i>)	0.0	0.0	0.3	0.3
House mouse (<i>Mus musculus</i>)	0.3	0.3	0.0	0.0
Total	54.0	5.5	31.6	2.7

habitat changes on rare or endangered species should not be ignored.

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Foraging Patterns of Tassel-Eared Squirrels in Selected Ponderosa Pine Stands¹

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The tassel-eared tree squirrel (*Sciurus aberti*) and its several subspecies, has a unique and apparent obligatory association with Southwestern ponderosa pine (*Pinus ponderosa*). The dietary dependence of these squirrels on pine, including inner bark and buds of terminal twigs and both staminate and ovulate cones, identifies the squirrel as an herbivore having a potentially major influence on the growth and reproduction of ponderosa pine. Conversely, extensive harvest of pine for wood products has resulted in deterioration of the squirrel's habitat since the turn of the century (Keith 1965).

A number of studies have attempted to explain the "boom and bust" population fluctuations that seem to be characteristic of tassel-eared squirrels. In his observations

on the ecology of Abert squirrels (*S. a. aberti*), Keith (1965) attributed short term fluctuations to changes in quantity and quality of major food items assumed to be provided by pine. However, high mortality in some years apparently resulted from some factors other than food. Hall (1981), in a study of Kaibab squirrels (*S. a. kaibabensis*) also observed population fluctuations. He suggested that seasonal differences in food resources and snowfall were potential causes of declines and recovery. Availability and use of various food items have not been adequately studied.

Stephenson (1974) in a study of Abert diets discovered that fungi were a major part of the total food consumed. The fungi in Stephenson's samples were identified as belonging to a subterranean group of mushrooms popularly called truffles (J. States, unpublished data), which are known to form mycorrhizal associations with pine roots. Some of these fungi were found to be new records for the Southwest (States 1983, 1984) and they were found to be primarily associated with blackjack age-class ponderosa pine stands with high canopy densities (States 1985).

A telltale sign of the activity of the tassel-eared squirrel is the presence of clipped twigs on the ground under a tree after the squirrel has removed the terminal shoot from a branch. The nutritional value of the inner bark consumed by the squirrel is low. A diet comprised solely of inner

Abstract.—Pine seed, primarily available in the fall, and hypogeous fungi, potentially available in all seasons, were major food items whose consumption was associated with an increase in biweekly body weights of marked squirrels. Use of alternative foods such as twigs (inner bark) and apical buds occurred when these food items were unavailable. Consumption of inner bark and buds was highest in winter (93%) and spring (86%). Although feed tree preference was noted, widespread feeding occurred in more than half of the trees in both study sites. The resulting variability in physical evidence of foraging suggests caution in its use for indexing squirrel population densities.

bark in the absence of supplemental foods could potentially threaten squirrel survival during adverse weather conditions (Patton 1974). The obvious selection of certain trees by squirrels for inner bark consumption supports the assumption that there are differences in quality of trees in the same stand. In a food preference study using captive Abert squirrels, Farentinos et al. (1981) were able to show a significant relationship between selective consumption of inner bark and low oleoresin content. However, Pederson and Welch (1987) noted a strong feeding preference for trees with inner bark that was easily peeled with no apparent relationship between inner bark oleoresin content and "feed tree" selection.

Studies on the impacts of squirrel herbivory on ponderosa pine have lead to mixed conclusions. Hall (1981) and Ffolliott and Patton (1978) found that heavy utilization of pine twigs had negligible effect on stand productivity, although Hall demonstrated significant growth decreases of individual feed trees. Soderquist (1987) reported twig clipping to decrease tree growth in ecotonal stands of ponderosa pine. Pearson (1950) and Larson and Schubert (1970) noted extensive, but seasonally variable, damage to cone crops. They were unable to determine the causes of the highly variable pattern of herbivory during several years of observation.

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The tassel-eared squirrel's variety of diet and use of the forest has lead to differences of opinion regarding the best management plan for both squirrel and forest. Patton et al. (1985) considered tree density, size, and patchy distribution to be major factors constituting habitat quality since squirrels use pine for cover and nesting as well as for food.

The purpose of this study was to determine the seasonal patterns of food resource utilization by Abert squirrels in selected ponderosa pine stands and to relate the results to squirrel population levels within the stands. The use of fungi and inner bark as major food items is discussed as it pertains to stand characteristics and the potential impact of herbivory on ponderosa pine.

Study Areas and Methods

Two sites in clumped, uneven-aged ponderosa pine stands were studied in areas that had not been disturbed by fire and timber harvest for the past 35 years. A 9.3 ha site was located on the property of the Lowell Observatory and adjacent to the Coconino National Forest. The other site of 2.5 ha was located in the Mount Elden Environmental Study area of the Coconino National Forest. The elevation of both sites was 2150 m, and they were within 10 km of the Flagstaff airport where weather data used in the study was collected (NOAA 1987).

Squirrels were captured, marked, and released at the observatory site. At this location there were 90 plots, 625 m² each, in a nested trapping grid similar to the one described by Patton et al. (1985). The grid contained 42 systematically spaced Tomahawk live-traps baited and set for eight daylight hours once each week. Trapping was conducted from September 1985 through June 1987 and squirrel body weight was recorded. Fecal pellets deposited in traps were collected and analyzed to

Table 1.—Estimated food availability for Abert squirrels.

Year	Truffles kg/ha	Seed cones/tree x n=25	Acorns/tree x n=20	Mushroom abundance
1983	2.88	144	552	high
1984	0.86	10	83	low
1985	0.39	10	123	very low
1986	0.72	137 ^a	20 ^b	very high
1987	0.65	10	10 ^b	moderate

^aCone crop 21% aborted due to insect damage; 31% of total cone crop harvested by September.

^bAcorn production low due to early frost.

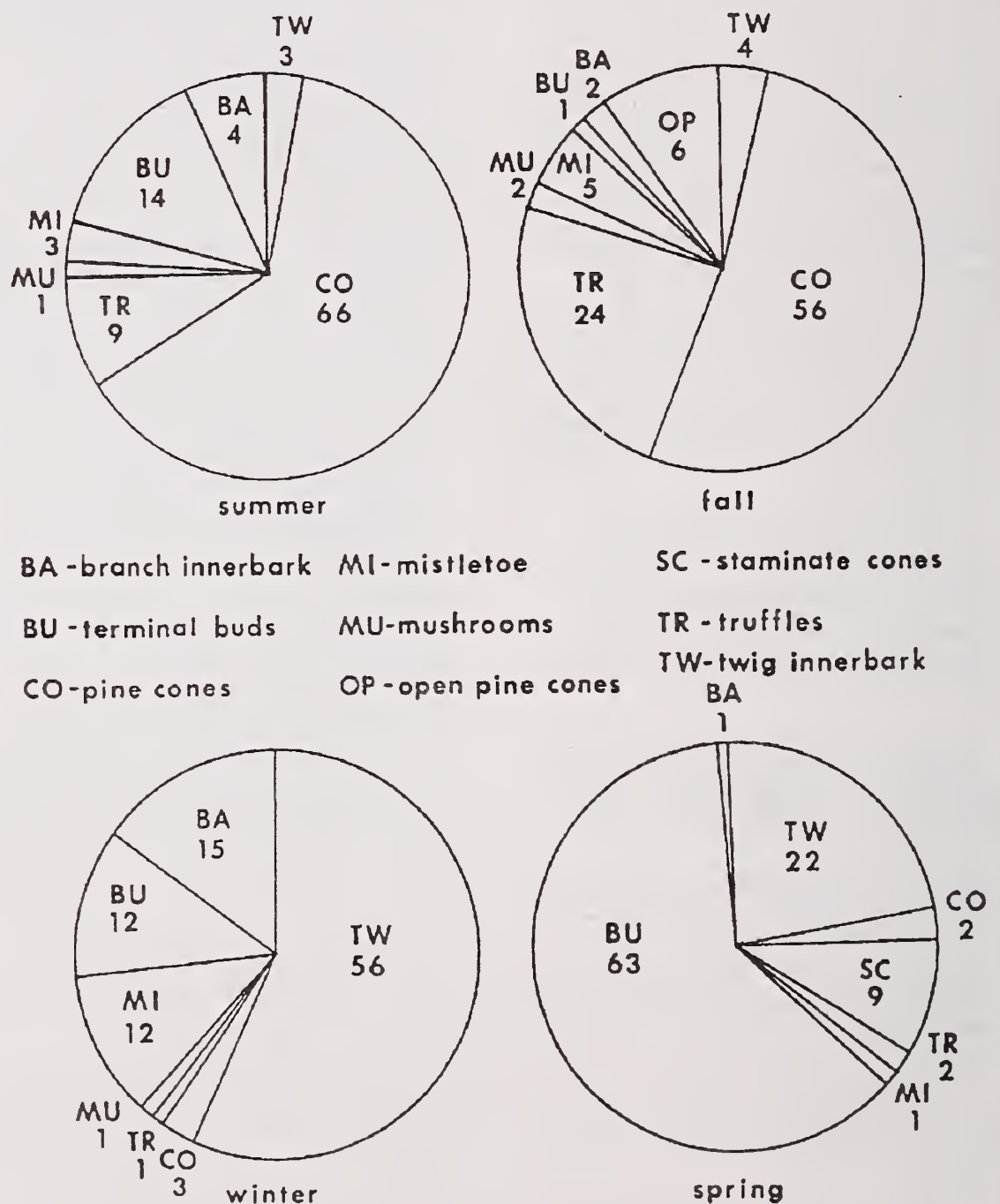


Figure 1.—Percentage of feeding time by Abert squirrels for each diet item in each season (from eighteen two-hour periods per season, Coconino National Forest, AZ).

determine the ratio of dietary fungus to plant matter and to identify the fungi through spore characteristics.

Observational data on foraging behavior was collected using focal animal sampling (Altmann 1974). We observed four individually marked males from July 1986 through November 1987 as they foraged in the study site. Data were collected in 18 two-hour observation periods in each of four "ecological" seasons. These seasons were established by combining months with similar temperature and precipitation means. The seasons correspond to periods of truffle production: Season I, December-March (winter); Season II, April-June

(spring); Season III, July-August (summer); Season IV, September-November (fall).

Resource availability and physical signs of foraging activity were recorded over a 20-month period (June 1986 through January 1988). Cone consumption, twig clipping, and digging activity were documented on 26 contiguous 625 m² plots (1.6 ha) on the observatory site. During each of the biweekly censuses, all twig remnants, cone cores, and digs (truffle excavations) were recorded with a notation of the nearest tree. Trees were characterized by age-class (blackjack, or yellow pine) and diameter at breast height (DBH). The

entire 2.5 ha Mount Elden site was sampled for seasonal foraging patterns. Permanently marked pines and oaks in 20 plots were censused yearly in September for acorn and cone production. Cones and acorns were counted on a quarter of the tree and multiplied by four to obtain a production estimate. Truffle production estimates were made according to States (1985). Relative mushroom abundance was determined by counting numbers of mushrooms present within 10 randomly placed 50 m² quadrats sampled in the fall.

Results

Resources available as food for tassel-eared squirrels showed considerable annual variability (table 1). The four food items were all relatively abundant in 1983, but availability subsequently dropped. Production of cones and mushrooms was relatively high again in 1986, but there were considerably fewer truffles and acorns present than in 1983. In general, the quantity of truffle production was more consistent than it was for the other foods.

Seasonal foraging behavior of the squirrels (fig. 1) reflected changes in availability of food items. The animals heavily utilized a large cone crop in 1986 before the seeds were mature, and continued to utilize it into November when the remaining seeds were released. Cone and truffle use dropped abruptly from a fall high of 80% feeding time when the squirrels switched to intensive feeding on buds and inner bark of twigs. This behavior comprised 85% of the spring feeding time. Collectively, pine products constituted the largest portion of the diet through winter and spring. Seasonal patterns were apparent in the use of different parts of the tree.

The physical evidence left in the forest by the squirrels verified a seasonal progression of food item availability (fig. 2). Numbers of digs

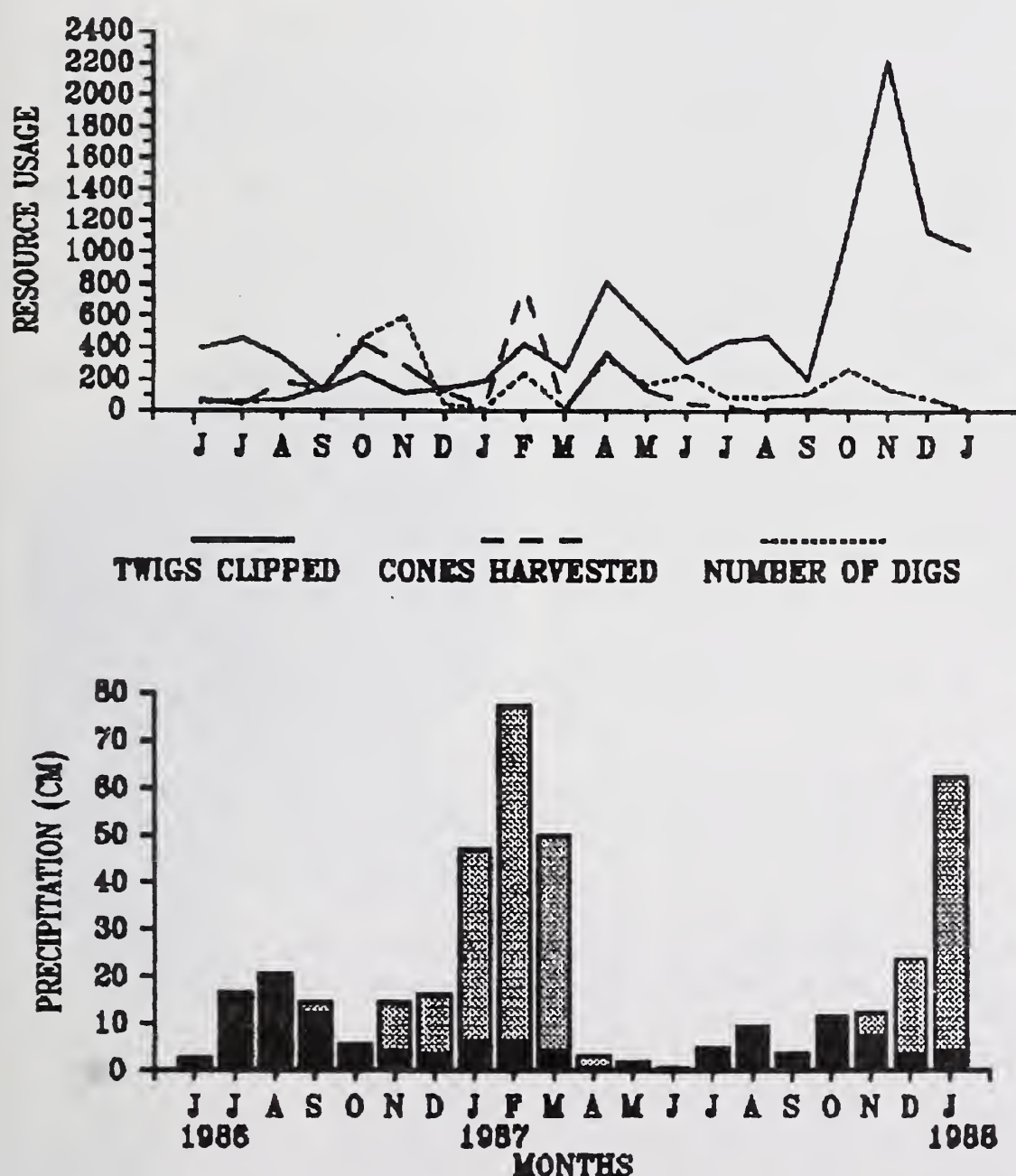


Figure 2.—Monthly resource usage by Abert squirrels compared to total precipitation (solid bar) and snow depth (shaded bar), Coconino National Forest, AZ.

peaked in late fall and dropped in the winter, a pattern which corresponds to foraging time percentages for truffles (fig. 1). Subsequent digs during winter and early spring represented retrieval of cones buried the previous fall. Numbers of cone cores left after seed removal increased as the cones matured. Numbers of cone cores subsequently decreased in the winter months. As the use of cones and truffles declined, numbers of clipped twigs increased. Twig clips decreased to a moderate level in summer but again reached a high level the following winter. This peak was coincident with increased snow depth, a decrease in availability of truffles, and the absence of seed cones. By the end of January 1988, a majority of the 1114 trees (67.9%) in the observatory site had been clipped at least once with an average of almost 10 clips per tree.

In spite of relatively low food availability in the year from September 1985 through August 1986 (table 1), resident squirrels maintained a fairly constant weight throughout the winter (table 2). The average weight of four male squirrels dropped 6% during spring and early summer from the previous fall's high. Subsequent weight gains, 5%, occurred concurrently with maturation of the 1986 fall cone crop. Winter weight loss paralleled the decrease in availability of fungi, as evidenced by their presence in fecal contents (fig. 3).

The number of terminal shoots removed by squirrels in the Mt. Elden site from 1984-1987 was apparently related to snowfall (table 3). Squirrel densities remained relatively constant, but the number of trees clipped increased by 30% and the average number of clips per tree decreased by 81%. Total snowfall was greater in 1985 than in either 1986 and 1987. The map of clipping behavior shows marked shifts in areas of heaviest clipping in the 2.5 ha site (fig. 4). The smallest area of clipping intensity (46% of the site) occurred in 1985, and it also had the highest

Table 2.—Mean body weight (grams) and standard deviation of individual male squirrels in each season from September 1985 through November 1986. The numbers of captures per season are in parentheses.

Squirrel	IV Fall	I Winter	II Spring	III Summer	IV Fall
1	614 + 11.7 (11)	632 + 30.1 (12)	610 + 12.7 (3)	587 + 27.9 (7)	610 + 27.6 (9)
2	748 + 37.0 (5)	680 + 34.3 (7)	723 + (1)	703 + 18.6 (5)	769 + 20.9 (5)
3	655 + 20.4 (13)	681 + 15.2 (12)	671 + 18.0 (7)	648 + 29.8 (5)	674 + 16.9 (8)
4	737 + 24.7 (6)	688 + 31.5 (5)	669 (1)	662 + 33.6 (7)	674 + 33.8 (11)
x	689	670	668	650	682

number of clips per tree. The area of clipping expanded in 1986 and 1987 to 67% and 64%, respectively. Of the 604 trees clipped in the three years, 45% were clipped once while 23%

were clipped every year. Yellow pine constituted 10% of the stand and 82% of these were clipped. Most yellow pines not clipped were isolated in open areas. Sixty-one percent of all

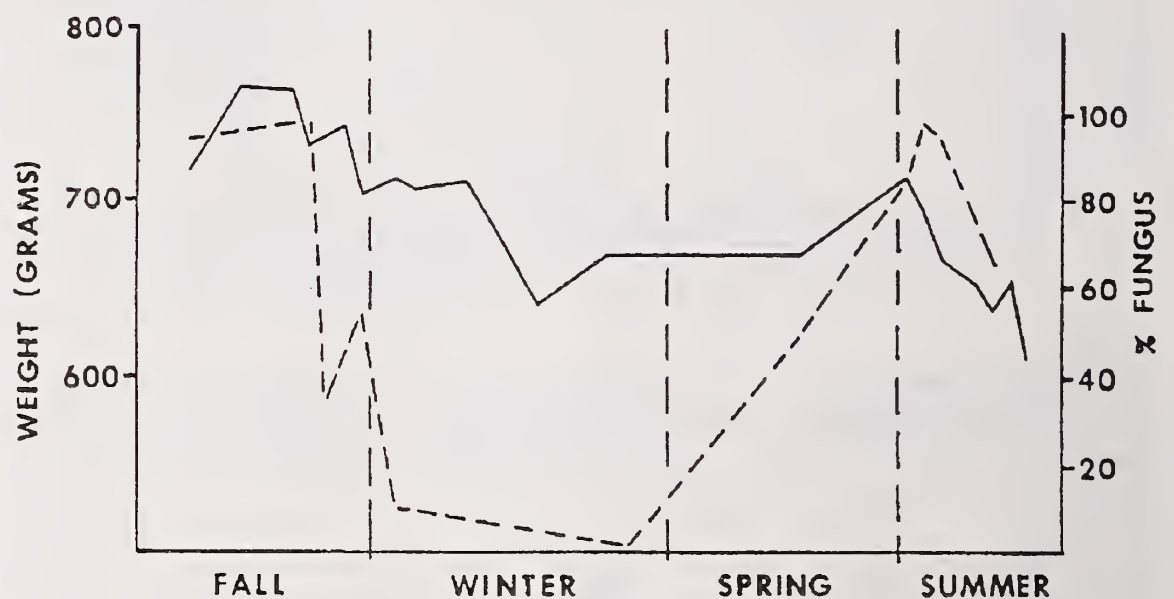


Figure 3.—Weight loss (solid line) by Abert squirrels as compared to fungal content of feces (dotted line) during the period September 1985 to August 1986, Coconino National Forest, AZ.

Table 3.—Twig clipping data for Yellowpine (YP) and Blackjack (BJ) age-class trees over three successive winter seasons in the Mount Elden study area.

Year	Snow cm.	Squirrel number	Number YP	Trees BJ	Clipped total	Clips/ tree	Total clips	Dry wt. kg
1984-85	345.4	6	38	155	193	124.7	24,061	295
1985-86	266.7	8	52	268	320	65.4	20,640	253
1986-87	217.7	6	58	533	591	24.2	14,288	175

blackjack pine with a DBH greater than 10 cm were clipped. Eleven of these and one yellow pine died following virtually total canopy removal by squirrels. The average number of twigs clipped in yellow pine was greater than in blackjack pine but their mean dry weight, 11.2 ± 8.7 g, was less than that of blackjack pine, 13.2 ± 4.8 g. Five of the yellow pines in 1985 had more than 1000 twigs removed from each. A majority of the trees clipped only once before 1987 were also clipped in 1987 and were located in an area with little previous squirrel use (fig. 4).

Discussion

The tassel-eared squirrel is a whole forest species in the sense that essentially all age classes of trees are utilized. Although pine provides much of the squirrel's food, the various items are taken by the squirrel from different age classes of trees (table 3). The largest number of cones is pro-

duced by mature yellow pines (Larson and Schubert 1970), while truffles tend to be associated with pole sized blackjack pines (States 1985). Thus, prime squirrel habitat provides optimal food in stands containing a combination of tree age classes whose size, density, and grouping provides cover and nesting sites as well (Patton 1984).

Major shifts in foraging by the tassel-eared squirrel are apparently associated with variations in the availability of food resources in the forest. In 1986 squirrels relied heavily on pine seeds with moderate utilization of truffles and the inner bark of twigs (fig. 2). Cone and acorn failure in 1987 resulted in a reversal of the relative emphasis on seeds and twigs. Observation of squirrel foraging revealed a corresponding opportunistic shift from such ephemeral foods as staminate cones and developing pine buds in the spring to mushrooms in summer to truffles in the fall. Similar opportunism in food utilization has also been reported for other tree squirrels: the European tassel-eared squirrel, *Sciurus vulgaris* (Wauters and Dhondt 1987), the American red squirrel, *Tamiasciurus hudsonicus* (Feron et al. 1986), and the western gray squirrel, *S. griseus* (Stienecker 1977).

In spite of a seasonal emphasis on temporary supplies of certain food items, the squirrel removed terminal shoots of ponderosa pine throughout the year. When cones and truffles became scarce, as in winter and early spring, squirrels increased consumption of inner bark (figs. 1 & 2). There seemed to be a clear preference for the inner bark of certain trees to the extent that some individual trees were nearly defoliated. However, a decreasing amount of snowfall in three years (table 3) was associated with an increasing number of trees from which inner bark was taken and a decreasing average number of clips per tree. Thus, the identification of a particular tree as a favorite "feed tree" (Ffolliott and Patton 1978) seemed to depend to some extent on

other relevant environmental conditions influencing access to food supplies, e.g., mobility over snow-covered ground.

The repeated use of individual trees for inner bark was surprisingly high. We found that 23% of all clipped trees had shoots removed in each of three years, while Ffolliott and Patton (1978) reported only 2% over four years of potential use. This difference between the two studies may have resulted from differences in squirrel population densities and/or from differences in the availability of alternative foods. Nevertheless, it is important to note that a resident squirrel population may not rotate feed trees to the extent previously reported. In addition, more than half a stand's individuals may become feed trees. We expect that continued observation will increase that percentage.

The quantity of hypogeous fungi remained a fairly consistent food supply, aside from its unusual abundance in 1983 (table 1). Truffles appear to be a common component of the diet of tree squirrels (Grönwall and Pehrson 1984, Moller 1983), if not of most small herbivorous mammals (Maser et al. 1978). Judging from the analysis of gut contents in this (Vireday 1984) and other squirrels (Grönwall and Pehrson 1984, Grachev and Fedosenko 1974, McKeever 1964), hypogeous fungi constitute one of the primary food resources. The drop in winter squirrel weight as inner bark replaced truffles in the diet (table 2 and fig. 1) is also suggestive of the importance of this fungal diet component. Kenward (1983) showed similar weight losses for gray squirrels, *S. carolinensis*, feeding heavily on inner bark.

Truffle production has been reported to be correlated with high canopy cover (States 1985), which is more characteristic of blackjack stands than of stands with a high proportion of yellow pines. This relationship between truffles and canopy cover may explain the preponder-



Figure 4.—Map of the 2.4 ha Mount Elden study site illustrating shifts in clipping intensity for each of three years (spring to spring), Coconino National Forest, AZ. Clipping data corresponding to these areas is presented in table 3.

ance of squirrel foraging activity observed in the blackjack stands.

Observations of food supply (table 3) and squirrel food use (fig. 2) showed considerable variability, much of it related to precipitation patterns. Consequently each year presented a different pattern of food combinations, which may take 5 to 10 years to repeat. Nevertheless, it is clear that squirrels clipped twigs to some extent every year, but greatly increased clipping when cones were scarce. Moreover, hypogeous fungi were a regularly used resource.

Management Implications

The number of twig clips found has been suggested as an index of squirrel population density (Brown 1982, Keith 1965). However, the complex pattern of clipping observed in these three years suggests some limitations. We advocate restricting such an index to comparisons of relative population densities between different sites within the same year, when one can reasonably presume that weather conditions, pine seed abundance, and availability of alternative foods to be similar over a large area.

Maintenance of clustered stands is essential to provide the canopy cover needed for truffle production as well as cover and nesting sites for squirrels. Reduction of stand heterogeneity and removal of trees in large disjunct blocks will likely have a negative impact on Abert squirrel habitat (see also Pederson et al. 1987). Over time, squirrels utilize a majority of blackjack and yellow pine within the stands. Forest management practices that provide corridors for squirrel movement among stands will potentially reduce localized herbivory and avoid severe tree damage.

Acknowledgments

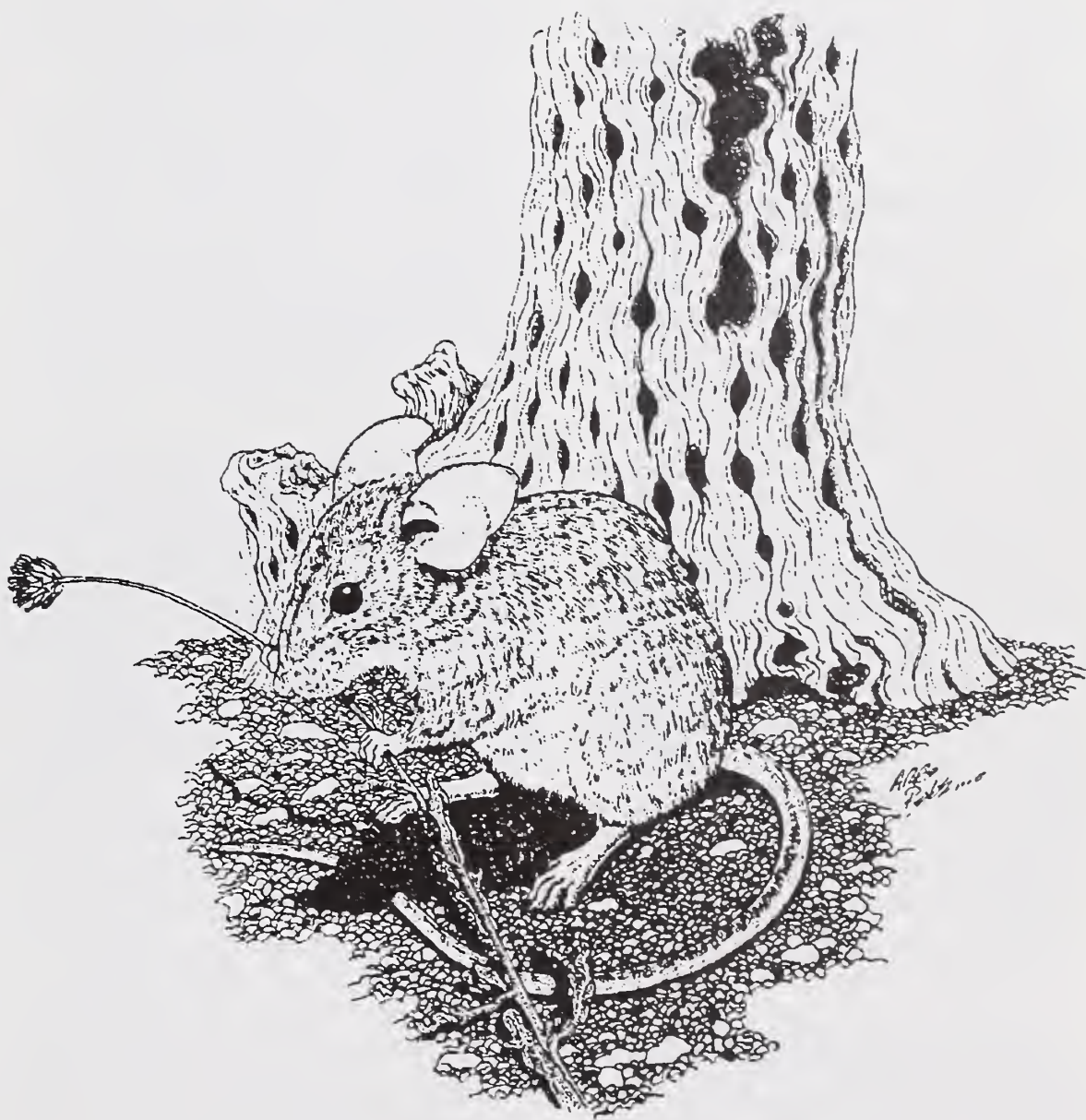
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Small Mammal Response to the Introduction of Cattle into a Cottonwood Floodplain¹

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Abstract.—Few differences between pastures in small mammal communities were evident prior to grazing, 1 month following grazing, and no differences in numbers or distribution of small mammals were observed 5 months following grazing. Each small mammal species exhibited different habitat use compared to availability and few habitat variables differed on grazed versus ungrazed pastures. Grazing at SCS recommendations in winter did not appear to have an initial effect on small mammal populations or their habitats in a Colorado floodplain.

Grazing by cattle in upland areas can affect vegetation and wildlife populations (Geier and Best 1980, Moulton et al. 1981, Madany and West 1983), but there is little understanding of how grazing influences wildlife populations and habitats in western riparian areas (Kaufman et al. 1982). Riparian areas of the western United States provide habitats for greater diversities and densities of wildlife than adjoining upland communities (Thomas et al. 1979, Knopf 1985), and livestock grazing is one of many uses that impacts riparian ecosystems.

Grazing of riparian zones generally occurs in winter along the South Platte River and similar stream or river systems in northeastern Colorado. Overgrazing is reported, and in some cases all ground cover including shrubs is removed (Beidleman 1954). The purpose of this study was to determine if small mammal communities and vegetation structure were similar in grazed and ungrazed

riparian areas in northeastern Colorado. The approach was to alter a riparian area experimentally by introducing cattle into an area that had not been grazed for 30 years. The specific objective was to contrast small mammal communities and vegetation structure before, during, and after grazing and between grazed and ungrazed communities.

Study Area and Methods

The study was conducted on the Colorado Division of Wildlife's Tamarack Ranch Unit, South Platte State Wildlife Area, in Logan County near Crook, Colorado, from March 1982 to August 1983. The climate is semi-arid. Mean annual precipitation is 47.4 cm and average monthly temperature is 22.1 C. Shallow clay-gravel soils in highly stratified alluvial deposits supported an overstory of mature plains cottonwood (*Populus sargentii*) and understories of shrubs (*Salix exigua*, *S. interior*, *Symphoricarpos occidentalis*, *Toxicodendron radicans*, *Vitis vulpina*, and *Rhus radicans*), forbs (*Phragmites communis*, *Spartina pectinatus*, *Chenopodium album*, *Conium maculatum*, *Rumex crispus*, and *Melilotus alba*), and grasses (*Elymus canadensis* and *Spartina pectinatus*).

The riparian zone adjoining the South Platte River was last grazed in the early 1950's (M. Gardner, pers. comm.). Ten 16-ha pastures were es-

tablished within the riparian zone and spaced at least 0.4 km apart to eliminate interactive effects among pastures. Five pastures selected at random were grazed from mid-November 1982 to mid-March 1983 at levels recommended by the U.S. Soil Conservation Service, with 35.5, 30.8, 9.0, 37.2, and 36.8 AUMs allocated. Pre-treatment data were collected on all pastures in March, June, and August 1982. Posttreatment data were collected on all pastures in March and August 1983.

A 100-trap grid of Sherman live traps with 15-m spacing between rows and columns (135 x 135 m, 2.25 ha) was established in each pasture to sample small mammal communities. Three, five-night trap sessions were scheduled per year: prior (middle March), during (late June), and after (late August) the peak small mammal breeding season. The total number of trap nights for the study was 25,000: 15,000 trap nights pretreatment and 10,000 trap nights post-treatment. Individuals were marked with a numbered aluminum ear tag, and species, sex, age, breeding condition, trap number, and weight were recorded. Density estimates were made using the computer program CAPTURE (Otis et al. 1978, White et al. 1982). CAPTURE examines capture-recapture data, gives population and density estimates for five different models, and indicates the model most appropriate for estimation. Model M (H) was de-

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terminated to be the most robust of the five estimators.

For each of the five trap sessions, trap sites were categorized according to trap success (no-capture vs. capture) and to the species captured at that site. In March 1982, five no-capture sites and five sites for each species were selected at random for vegetation sampling within each pasture. Beginning in June 1982 and thereafter, the sample size per pasture was increased to ten no-capture sites and ten capture sites for each species.

Habitat variables were measured using two line intercept transects 5-m in length at each selected trap site. Variables included percentage cover of sand, litter, grass, forb, and shrub along the 5-m transect. Transects were centered on the trap site and oriented toward randomly chosen cardinal compass directions (north, south, east, or west). The linear intercept of each variable with the

transect was measured with an incremental tape. Two additional measurements at each trap site were distance-to-nearest-understory (<10 m) and distance-to-nearest-overstory (>10 m). Vegetation sampling occurred concurrently or immediately following each trap session.

Chi-square tests were used to test for pretreatment differences in species composition among those pastures chosen for grazing and those chosen for controls. Chi-square tests were also used to evaluate posttreatment data. A *t*-test was performed to examine differences in mean body weight between treatment groups.

T-tests were used to compare habitat variables between species and between species-specific capture sites from all other trap locations. In each season, the vegetation variables associated with the capture sites of a species were compared to the pooled sample of vegetation variables consisting of no-capture sites in addition

to sites for all other species (Dueser and Shugart 1978). The degree of habitat specificity was indicated by the number of variables for which the species sample differed from the pooled sample. Following the species-specific and pooled sample two-group comparison, mean vegetation values associated with each species were compared on grazed and control pastures using *t*-tests. These procedures determined whether habitat used by a specific species differed from the average habitat available and compared a species habitat use on control and grazed areas regardless of habitat availability. Some overlap in use of trap sites was observed, thus the pooled sample is not expected to be completely distinct from the species specific sample (Dueser and Shugart 1978).

All statistical tests and density estimates were performed using the Statistical Package for the Social Sciences (Nie et al. 1975).

Results

Species Composition

Nine species of small mammals were captured in 1982 and 1983 (table 1). The deer mouse (*Peromyscus maniculatus*) was the most abundant species, with the western harvest mouse (*Reithrodontomys megalotis*), kangaroo rat (*Dipodomys ordii*), prairie vole (*Microtus ochogaster*), house mouse (*Mus musculus*), hispid pocket mouse (*Perognathus hispidus*), northern grasshopper mouse (*Onychomys leucogaster*), masked shrew (*Sorex cinereus*), and spotted skunk (*Spilogale putorius*) comprising less than 2 % of the 9,304 captures.

Pretreatment species richness did not differ among grazed versus ungrazed in March 1982 ($X^2 = 2.47$, $P = 0.650$) but significant were evident in June ($X^2 = 15.39$, $P = 0.017$) and August ($X^2 = 33.18$, $P = 0.001$) (table 1). The differences in June and August were caused by the abundance of

Table 1.—Total numbers of small mammals captured in grazed vs. ungrazed pastures, March 1982 to August 1983, South Platte River Wildlife Management Area, near Crook Colorado.

Species/ Treatment	Pretreatment			Posttreatment	
	March	June	August	March	August
Deer Mouse					
Control	297	¹ 372	² 427	³ 268	104
Grazed	498	609	575	344	155
Western Harvest Mouse					
Control	19	24	27	45	9
Grazed	39	27	22	40	3
Prairie Vole					
Control	5	5	12	11	3
Grazed	4	7	2	4	6
Kangaroo Rat					
Control	3	12	9	10	0
Grazed	3	3	0	0	0
Other ³					
Control	6	7	17	2	5
Grazed	7	5	6	6	9

¹Significantly different than other treatment ($P < .05$).

²Significantly different than other treatment ($P < .001$).

³Includes house mouse, hispid pocket mouse, northern grasshopper mouse, masked shrew, and spotted skunk.

kangaroo rats, prairie voles, and house mice on control pastures. While three species—the hispid pocket mouse, masked shrew, and spotted skunk—were found only on pastures to be grazed. Number of captures of the two common species, the deer mouse and western harvest mouse, were not different in June ($X^2 = 1.71$, $P = 0.187$) or August ($X^2 = 2.97$, $P = 0.091$) between pastures to be grazed and control pastures.

Following nearly 4 months of grazing, the composition of small mammal communities in control versus grazed pastures differed in March 1983 ($X^2 = 15.9$, $P = 0.001$) (table 1) but not in August ($X^2 = 6.05$, $P = 0.109$). The kangaroo rat was not captured on treated pastures in March or August 1983 although present in two of five pastures prior to treatment in 1982. The number of harvest mice captured in grazed pastures increased markedly from March 1982 to March 1983 (19 vs. 45) in contrast to control pastures (39 vs. 40).

Inundation of all pastures in May-July 1983 (see Knopf and Sedgwick 1987) appeared to influence species distributions and abundances in August. From March to August captures of deer mice on all pastures declined from 611 to 259, western harvest mouse from 85 to 12, and kangaroo rats and mask shrews were no longer captured.

Densities and Population Structures

Only the deer mouse was captured in sufficient numbers to calculate densities accurately. Deer mice densities were consistently higher on grazed pastures before and after treatment (table 2). However, the density of deer mice decreased 18.7% from pre- to posttreatment on the five control pastures ($x = 33.6/\text{ha}$ vs. $x = 27.3/\text{ha}$) versus 42.9% on the five treated pastures ($63.2/\text{ha}$ vs. $36.1/\text{ha}$) for the same interval.

Age ratios appear unaffected by grazing (table 2). In contrast, sex ratios in deer mice shifted significantly following grazing ($X^2 = 4.90$, $P = 0.049$) with three of five grazed pastures having substantially more males. Western harvest mice sex ratios also changed following grazing, with a higher percentage of females captured, but sample sizes were insufficient for separate tests on each of the 10 pastures.

The percentage of female deer mice in breeding condition was similar on all pastures prior to grazing except in June 1982, when a higher percentage of females ($X^2 = 3.84$, $P = 0.049$) were in breeding condition on control pastures. Following grazing, the percentage of breeding females was higher in March ($X^2 = 5.53$, $P = 0.019$) on control pastures yet grazed pastures had a higher percentage of breeding females ($X^2 = 5.44$, $P = 0.020$) in August 1983. No significant

differences in the percentage of breeding males or females between treatment groups was observed for the other species.

Deer mice body weights were similar across pastures prior to grazing, except in June ($t = 3.18$, $P = 0.002$). After treatment, mean body weights for mature (subadult plus adult) deer mice were significantly less ($t = 2.66$, $P = 0.008$) on grazed pastures ($18.56 \pm 0.18\text{g}$) than on ungrazed pastures ($19.3 \pm 0.21\text{g}$) when data from all replicates were combined. The divergence in mean deer mouse body weight between control and grazed pastures continued into August 1983 ($t = 3.02$, $P = 0.003$).

Species Habitat Use

Only sample sizes for the deer mouse, western harvest mouse, prairie vole, and kangaroo rat were suffi-

Table 2.—Selected population characteristics including population density (mean no. per ha), age ratio (% juveniles), sex ratio (% females), and breeding condition (% breeding females), March 1982 to August 1983, South Platte River Wildlife Area, near Crook Colorado.

Characteristic/ Species/ Treatment	Pretreatment			Posttreatment	
	Mar 1982	Jun 1982	Aug 1982	Mar 1983	Aug 1983
Density					
Deer Mouse					
Control	33.6	36.3	27.3	18.7	24.8
Grazed	63.2	55.3	36.1	42.7	24.7
Age Ratios					
Deer Mouse					
Control	1.3	5.3	1.9		
Grazed	0.7	4.4	4.3 ¹		
Sex Ratios					
Deer Mouse					
Control		46.0	48.8	48.7	44.0
Grazed		53.0	51.3	46.2	43.8
Western Harvest Mouse					
Control		60.9	52.0	31.6	0.0
Grazed		37.0	31.8	42.5	0.0
Breeding Condition					
Deer Mouse					
Control		65.8	67.8	16.2	64.6
Grazed		49.0 ¹	69.5	6.61	85.1 ¹

¹Significantly different than other treatment ($P < 0.05$).

cient for subsequent analysis. Habitat use by deer mice differed from that available in 34% (12/35) of the *t* tests on control pastures and 12% (4/35) of the tests on grazed pastures over all seasons (table 3). Deer mice were most frequently associated with a lower percentage of grass cover and litter as well as presence of shrubs. Although habitat near deer mouse capture sites differed from that available, habitat use was similar on control and grazed pastures. Among those habitat variables associated with the deer mouse, 66.7% (2/3) in March 1982, 100% (2/2) in June 1982, 66.7% (2/3) in August 1982, 80% (4/5) in March 1983, and 0% (0/5) in August 1983 were similar on control and grazed pastures.

Like deer mice, the harvest mouse used habitats differing from those available and preferred similar sites on control and grazed pastures (table 4). Thirty-four percent (12/35) of the tests on control pastures and 37% (13/25) of the tests on grazed pastures were significantly different whereas the majority (68%, 13/19) had similar values on control and grazed pastures. The occurrence of harvest mice was most strongly associated with a high percentage of litter and grass cover and a low percentage of sand around the capture site.

Prairie vole capture sites differed from the average available site for only 11% (4/35) of the habitat comparisons on control pastures and 17% (6/35) of the habitat comparisons on

grazed pastures (table 5). Prairie vole habitat was similar to habitat used by western harvest mouse, as both exhibited a preference for sites with a high percentage of litter. For vegetation variables which were significantly different on prairie vole capture sites compared to the pooled sample of sites, 88% (7/9) had similar values on control and grazed pastures.

Kangaroo rats exhibited the highest habitat specificity among the four major mammal species (table 6). Habitat variables from kangaroo rat capture sites differed from the pooled sample of sites for 64% (18/28) of the habitat comparisons on control pastures and 50% (7/14) of the comparisons on pastures to be grazed. The factors which appeared most critical in determining the distribution of kangaroo rats was the high percentage of sand, moderately high percentage of forbs, and low percentages of litter and grass.

Table 3.—Comparison of mean vegetation values between deer mouse capture sites and the pooled sample on grazed and ungrazed pastures, March 1982 to August 1983, South Platte River Wildlife Management Area, near Crook Colorado.

Variable/ Treatment	Pretreatment			Posttreatment	
	Mar 1982	Jun 1982	Aug 1982	Mar 1983	Aug 1983
Sand (%)					
Control	16.9	4.4 ¹	8.1	3.3	20.1
Grazed	7.5	6.1	4.7 ¹	2.1	10.7 ²
Litter (%)					
Control	74.41	71.4	86.2 ¹	89.8	24.9
Grazed	83.5	79.4	88.7	87.3 ¹	21.8
Grass (%)					
Control	20.6 ¹	32.9	52.9	38.1 ¹	23.5 ¹
Grazed	37.3 ²	46.6 ²	68.1	53.5 ²	43.2 ²
Forb (%)					
Control	16.4	48.7	55.2	30.9	18.5 ¹
Grazed	19.4	38.2 ²	41.5 ²	23.4 ²	25.7 ²
Shrub (%)					
Control	6.9	10.3	17.2	20.9 ¹	31.4 ¹
Grazed	12.0	15.6	25.4	23.8	16.3 ²
Disto ³					
Control	12.3 ¹	11.8	10.6	13.5 ¹	10.0
Grazed	9.4	10.3	12.2	12.0	21.1 ^{1,2}
Distu ⁴					
Control	5.5	3.1 ¹	3.5	2.8	1.2 ¹
Grazed	7.1	3.0	1.9 ^{1,2}	2.04.4 ²	

¹Significant ($P < 0.05$) difference between deer mouse capture sites and pooled sample.

²Significant ($P < 0.05$) difference between grazed and control pastures.

³Distance to nearest overstory ($>10m$).

⁴Distance to nearest understory ($<10m$).

Discussion and Conclusions

Kaufman et al. (1982) in Oregon noted that small mammal densities decreased just following grazing only to increase to pre-grazing levels within a year. Riparian grazing in Oregon, as in most western rangelands, is often in late spring to early fall. A similar pattern, however, is evident following winter grazing in a riparian area in northeastern Colorado with few detectable differences observed in small mammal community 5 months following grazing.

The elimination of kangaroo rats from grazed areas appears to be a consequence of grazing although they were never really abundant on pastures to be grazed (table 1). In sandhill rangeland of eastern Colorado, Green (1969) found the density of kangaroo rats approximately the same on ungrazed and grazed pastures. Kangaroo rats may not have colonized riparian grazed pastures because of a change in microhabitat

prior to, or unrelated to, cattle introduction. Regardless, the riparian zone appeared to be a marginal habitat for this upland species.

Differences in age ratios appear unrelated to grazing. Abramsky (1976) found that juvenile deer mice do not readily enter traps and, thus, may be under represented in age-class ratios. The Trivers-Willard hypothesis suggests that a population under stress will produce an increased proportion of females (Myers 1978). The imbalance in deer mouse sex ratios observed in this study on grazed, but not control pastures, does not appear to be related to change in primary sex ratio or survival of young as suggested by the above hypotheses. Rather, most animals captured in March 1983 trap session were adults, 70% of which were tagged in 1982. The mean body weight of deer mice on grazed pastures following treatment was lower than on control pastures. A more parsimonious hypothesis for the observed shift in sex ratio is emigration of females. Bowers and Smith (1979) found that female deer mice inhabit more mesic microhabitats than males. Grazing by cattle may have altered microhabitats preferred by females and or other resources, particularly seeds, may have been more abundant on control areas. There is substantial evidence in other studies that deer mouse populations are limited by seasonal food availability (Gashwiller 1979), specifically in winter (Taitt 1981).

Small mammal habitat use and seasonal habitat shifts were similar on grazed and control pastures. Each species illustrated differential habitat use compared to availability, and patterns in habitat use were little affected by grazing. Deer mice habitat, largely areas with little grass cover, was consistently distinguishable from that of other species as reported elsewhere (Bowers and Smith 1979, Kantak 1983, Lovell 1983). Habitat use and number of captures of the western harvest mouse, prairie vole,

and kangaroo rat reported in this study are also consistent with that previously documented. The western harvest mouse is reported to be closely associated with grassy sites (Hill and Hubbard 1943, Lovell 1983) and use of sandy sites by kangaroo rats was noted by Green (1969). The importance of vegetative cover to the prairie vole has been well documented (Birney et al. 1976, Green 1969).

In summary, research reported in this paper was conducted in an experimental framework, with five replications, to evaluate the initial effects of cattle grazing in winter on small mammal community in a riparian area. Winter grazing of riparian areas based on Soil Conservation Service

recommended levels appears to have little initial effect on small mammal populations and their habitats. The study further indicates that pretreatment assessment of habitat and small mammal populations in studies to evaluate effects of grazing in riparian areas is important. Significant differences in small mammal numbers and species-specific habitat use observed following grazing could have been attributed to treatment without knowledge of pretreatment population and habitat conditions.

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Table 4.—Comparison of mean vegetation values (%) between western harvest mouse capture sites and the pooled sample on grazed and ungrazed pastures, March 1982 to August 1983, South Platte River Wildlife Management Area, near Crook Colorado.

Treatment	Pretreatment			Posttreatment	
	Mar 1982	Jun 1982	Aug 1982	Mar 1983	Aug 1983
Sand (%)					
Control	0.0 ¹	0.1 ¹	5.5	0.3 ¹	12.9
Grazed	5.9	1.8 ¹	0.0	0.2	0.0 ²
Litter (%)					
Control	95.4 ¹	73.8	89.9 ¹	93.4 ¹	42.6
Grazed	93.1	58.4 ¹	89.2	95.0 ¹	16.0
Grass (%)					
Control	61.1 ¹	40.3	64.4	78.2	43.2
Grazed	78.6 ^{1,2}	53.6	78.0	79.7 ¹	55.0
Forb (%)					
Control	19.9	49.6	53.0	20.2 ¹	28.2
Grazed	14.8	35.5 ²	38.6	12.2 ^{1,2}	38.7
Shrub (%)					
Control	11.6	20.5 ¹	22.8	8.8 ¹	22.2
Grazed	4.8 ¹	14.3	30.1	25.2	26.7
Disto ³					
Control	9.1	12.2	8.9	11.7	6.9 ¹
Grazed	8.6	11.4	14.1 ¹	12.9 ¹	65.0
Distu ⁴					
Control	7.2	5.1	2.7	3.6 ¹	1.4
Grazed	7.6	4.7 ¹	1.3 ¹	1.5 ²	4.8

¹Significant ($P < 0.05$) difference between western harvest mouse capture sites and pooled sample.

²Significant ($P < 0.05$) difference between grazed and control pastures.

³Distance to nearest overstory ($> 10m$).

⁴Distance to nearest understory ($< 10m$).

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Table 5.—Comparison of mean vegetation values between prairie vole capture sites and the pooled sample on grazed and ungrazed pastures, March 1982 to August 1983, South Platte River Wildlife Management Area, near Crook Colorado.

Treatment	Pretreatment			Posttreatment	
	Mar 1982	Jun 1982	Aug 1982	Mar 1983	Aug 1983
Sand (%)					
Control	0.0	20.0	13.9	0.0	0.0
Grazed	0.0	0.0	0.0 ¹	0.0	0.0
Litter (%)					
Control	88.0	80.0	85.4	71.0	100.0
Grazed	99.7 ^{1,2}	85.7	84.5	99.5 ¹	33.5
Grass (%)					
Control	52.2	52.6	36.6	80.0	100.0
Grazed	78.7 ¹	43.4	56.0	65.0	63.7
Forb (%)					
Control	25.0	42.8	49.0	2.0	100.0
Grazed	22.8	29.9 ²	21.0	38.0	40.7 ²
Shrub (%)					
Control	0.0	4.8	48.6 ¹	22.0	0.0
Grazed	5.3	17.3	22.5	20.6	23.0
Disto ³					
Control	5.8 ¹	14.1	10.9	2.4	15.0
Grazed	15.6 ^{1,2}	10.6	4.0 ^{1,2}	12.4	95.7 ¹
Distu ⁴					
Control	5.8	2.4	0.2 ¹	3.2	7.5
Grazed	14.0	1.8	5.6 ²	2.7	12.8

¹Significant (P < 0.05) difference between the prairie vole and pooled sample.

²Significant (P < 0.05) difference between grazed and control pastures.

³Distance to nearest overstory (>10m).

⁴Distance to nearest understory (<10m).

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Table 6.—Comparison of mean vegetation values between kangaroo rat capture sites and the pooled sample on grazed and ungrazed pastures, March 1982 to August 1983, South Platte River Wildlife Management Area, near Crook Colorado.

Treatment	Pretreatment			Posttreatment	
	Mar 1982	Jun 1982	Aug 1982	Mar 1983	Aug 1983
Sand (%)					
Control	53.0 ¹	67.4 ¹	38.6 ¹	34.9 ¹	
Grazed	53.0 ¹	51.0 ¹			
Litter (%)					
Control	69.0	44.4 ¹	56.5 ¹	49.7 ¹	
Grazed	38.0 ¹	70.0			
Grass (%)					
Control	12.0	10.7 ¹	29.4 ¹	15.1 ¹	
Grazed	33.7	11.0 ¹			
Forb (%)					
Control	18.0	71.1 ¹	65.6	44.8 ¹	
Grazed	25.3	60.5			
Shrub (%)					
Control	21.5	1.1 ¹	10.1 ¹	4.2 ¹	
Grazed	10.7	26.0			
Disto ²					
Control	3.6 ¹	11.2	6.7 ¹	9.8	
Grazed	7.5	6.0 ¹			
Distu ³					
Control	9.6	7.5 ¹	5.1 ¹	4.3	
Grazed	3.2 ¹	0.4 ¹			

¹Significant ($P < 0.05$) difference between kangaroo rat capture sites and pooled sample.

²Distance to nearest overstory (>10m).

³Distance to nearest understory (<10m).

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Old Growth Forests and the Distribution of the Terrestrial Herpetofauna¹

Hartwell H. Welsh, Jr.² and Amy J. Lind³

The coniferous forests of the Pacific Northwest are currently the focus of a national conflict between competing interests. These ancient forests, previously more species rich and continuous across the continental United States, have undergone a natural decline since the Mesozoic in conjunction with broad climatic and geologic changes (Axelrod 1976). This process eliminated most of the wooded areas of the Midwest, but left expansive tracts of forest in the eastern and western United States. In the last hundred years, many of these remaining ancient forests have been harvested for wood products, changing the species composition, structure, and forest age (Harris 1984). These natural forest ecosystems have been altered so rapidly that we are only now recognizing the loss of some plant and animal species and the threat to others [e.g., the spotted owl (*Strix occidentalis*)] (Simberloff 1987). Recent concern for the health and well-being of these forest ecosystems, and the need for more knowl-

edge to meet management goals and the requirements of the National Forest Management Act 1976 and the Endangered Species Act 1973 has prompted research into the structure and composition of the vertebrate communities of these forests (Meslow et al. 1981, Raphael 1984, Ruggiero and Carey 1984).

From 1981 through 1983, Raphael (1984, 1987, this volume) used a variety of sampling methods to collect data on the forest age, moisture, and habitat associations of birds, mammals, reptiles, and amphibians in forests of northwestern California. From 1984 through 1986, researchers from the Forest Service's Pacific Southwest Forest and Range Experiment Station extended these studies to include southwestern Oregon. By measuring differences in the species composition and relative abundance of the herpetofaunal community in altered versus unaltered habitats it is possible to indicate biologically meaningful differences in habitat quality (e.g., Bury et al. 1977, Busack and Bury 1974, Jones 1981, Luckenbach and Bury 1983, Ortega et al. 1982). Such information on differences in the composition of the herpetofauna, relative to forest age and moisture, have scientific value as well as practical value, as indicators of habitat change, useful to natural resource managers.

This paper reports on a study to determine the occurrence and abundance of the forest herpetofauna rela-

Abstract.—Terrestrial herpetofauna were sampled by pitfall traps and time-constrained searches on 42 stands of Douglas-fir/hardwood forest in southwestern Oregon and northwestern California. Stands ranged in age from 40 to 450 years. We found 25 species of herpetofauna. Species diversity was greater in older forest stands than in young stands. Amphibians were significantly more abundant in old than in young stands and significantly less abundant in dry than in moist stands. Our research indicates that changes in forest structure due to forest practices results in reduced species diversity and abundance among the herpetofauna.



Figure 1.—Study stands in Douglas-fir forests were located in northwestern California and southwestern Oregon. Triangles = stands in the inland area, circles = stands in the coastal area.

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tive to forest age and moisture, and to compare two methods (time-constrained searches and pit-fall trapping) used to sample this herpetofauna in northwestern California and southwestern Oregon.

STUDY AREA

This study was conducted in Douglas-fir (*Pseudotsuga menziesii*)/hardwood forests at low to mid-elevations in the Klamath Mountains and Coast Range. We sampled 54 stands, but we use data from only 42 stands, omitting nine higher elevation, white-fir dominated, stands and three stands on serpentine soils because they differed so greatly from our remaining stands. Even-aged stands in the above forest type were selected in three areas within the Klamath Mountains and Coast Range (fig. 1) in accordance with procedures outlined by Spies et al. (in press). Using stand characteristics (Franklin et al. 1986) and tree age, we assigned stands to one of three age classes: young, mature, and old-growth forests. Stands ranged in age from 40 to 450 years. Stands in old-growth were further categorized into three moisture classes: dry, mesic, and wet (fig. 2). Stands ranged in size from 21 to 150 hectares, and in elevation from 53 m to 1205 m. One-half of the stands occurred within the Coast Range, an area formed primarily of Franciscan parent materials and dominated by the maritime climatic influences of the Pacific Ocean. These stands were classified as coastal forest stands (fig. 1). All stands were dominated by Douglas-fir and con-

Old Growth Dry:	Old Growth Mesic:	Old Growth Wet:
1 coastal 3 inland	4 coastal 6 inland	3 coastal 3 inland
	Mature:	
	5 coastal 6 inland	
	Young:	
	8 coastal 3 inland	

← Moisture Class →

↑
Age
Class
↓

Figure 2.—Distribution of study stands by forest age and moisture class, and by coastal and inland area.

tained a significant hardwood element, primarily tanoak (*Lithocarpus densiflora*) and madrone (*Arbutus menziesii*); about half also contained coast redwood (*Sequoia sempervirens*).

The other sites were designated inland stands (fig. 1), occurring within the Klamath Mountains, primarily on granitic and metamorphic parent materials. This area is subject to colder winters and drier, hotter summers than the Coast Range. The

inlands stands were dominated by Douglas-fir in association with tanoak, madrone, and to a lesser extent, canyon live oak (*Quercus chrysolepis*), black oak (*Quercus kelloggii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and incense cedar (*Calocedrus decurrens*). For a more complete description of the vegetations of these two provinces see Raphael (in press) and Sawyer and Thornburgh (1977).

Table 1.—Structural features¹ of Douglas-fir stands on which herpetofauna were sampled in northwestern California and southwestern Oregon.²

Structural feature	Forest age class		
	Young (9) ³ < 100 yrs (mean ⁴)	Mature (11) 100-200 yrs (mean)	Old (19) > 200 yrs (mean)
Live trees			
Age of dominant size class of Douglas-fir	44.3 ±18.3	129.0 ±38.9	264.6 ±74.4
Diameter at breast height (DBH) of dominant size class of Douglas-fir (cm)	38.4 ±14.8	85.1 ±22.2	111.5 ±23.8
lg. conifers—trees/ha	1.5	17.1	34.7
(> 80 cm DBH)	±2.1	±12.0	±14.1
lg. hardwoods—trees/ha	9.1	10.7	13.0
(> 50 cm DBH)	±10.8	±12.0	±10.1
sm. trees—trees/ha	1430.0	764.1	630.0
(conf.—5-80 cm DBH + hdwds—5-50 cm DBH)	±594.0	±331.0	±240.0
Snags (conifers and hardwoods)			
large—snags/ha	3.4	2.2	6.1
(> 50 cm DBH and > 4.5 m in height)	±6.3	±2.2	±5.9
Logs			
lg. conifers—logs/ha	1.3	0.7	4.0
(> 50 cm DBH and > 15 m long)	±4.0	±1.8	±4.0
lg. conifers—mt/ha ⁵	1.2	1.0	6.9
	±3.5	±2.5	±6.9
sm. conifers—logs/ha	334.4	151.4	192.2
	±179.5	±129.9	±107.8
hardwoods—logs/ha	95.6	146.4	113.7
	±64.8	±123.1	±59.0

¹Bruce Bingham, unpublished data on file with Pacific Southwest Forest and Range Experiment Station, 1700 Bayview Drive, Arcata, CA 95521.

²Sampling occurred from 1984-1986.

³Number of stands.

⁴Mean ± 1 standard deviation.

⁵mt = metric tons.

METHODS

Herpetofauna Sampling

A herpetofaunal sampling design was developed for the USDA Forest Service's old-growth wildlife habitats project in Oregon and Washington by Corn and Bury (in prep.). Their design used two methods to sample species composition and relative abundance of the herpetofauna: pitfall traps (PF) and time-constrained searches (TCS) (Bury and Corn, this volume; Welsh 1987). The TCS method employed in our study differed from that described by Corn and Bury (in prep.) in that headwater habitats (springs, seeps, and first order streams) were included in the sampling. Pitfall trap grids consisted of 36 cans buried at ground level and spaced 15 m apart. Traps were covered with bark or cedar shakes. We sampled 40 stands in the fall of 1984 and 1985, for 50 and 30 nights, respectively. Our total pitfall trapping effort amounted to 115,200 trap-nights. Time-constrained searches consisted of intensively searching all terrestrial microhabitats in the forest environment for a fixed amount of time. Only actual search time was counted, when an animal was encountered the timer was stopped while data were collected. A 4-person-hour TCS was conducted on each of the 42 stands in 1984 and 1985. An additional 4-person-hour TCS was conducted on 30 stands in 1986. Our total effort for TCS amounted to 456 person-hours.

Forest Age

Forest age was determined for each stand by increment borer, or by counting rings on stumps in adjacent logged areas. Dominant or co-dominant size class Douglas-fir trees were selected for aging and trees were cored at breast height. Two to 10 trees (average 3) were cored on each stand and the sample mean was used

to estimate forest age for the stand. On the basis of tree coring, ring counts, and structural characteristics (Franklin et al. 1986), we grouped stands into three age classes: young forest, <100 years; mature forest, 100-200 years; and old-growth forest, 200+ years (table 1).

Moisture Class

Stands that were classified as old-growth were also assigned a moisture classification (dry, mesic, or wet), depending on plant species composition and percent cover of the herb and shrub layers within the stand. The data were independently recorded from three to five 0.1 ha circular plots selected at random within each stand. Moisture class assignment was based on mean percent cover values and the absolute constancy of particular shrub and herb species within each stand.

Faunal Comparisons

We tested the null hypotheses (H_0) that mean capture frequencies for herpetofauna did not differ between either forest age or moisture classes (1) within the coastal and inland areas, (2) between the coastal and inland areas, and (3) among all stands (coastal and inland areas combined). Only the mesic old-growth stands were used in the age analysis (fig. 2). One coastal old-growth dry stand prevented testing for differences in means among moisture classes within the coastal area, and between the coastal and inland dry stands.

We emphasize that our inferences are drawn from observations and not experimental manipulations. Though our results are described in the context of hypothesis testing, our study is primarily exploratory. In addition, the power of our tests was low because our sample sizes were relatively small. Our approach yields preliminary results about forest age

and moisture relationships among the herpetofauna, but we caution against making broad inferences.

Combining Data Across Years

Data from pitfall trapping were totaled, by stand, for each species, divided by 50 (1984 data) or 30 (1985 data) nights x 36 traps and multiplied by 1000 to yield captures per 1000 trap-nights. Data from time-constrained searches were adjusted for unequal sampling effort by expressing abundance of each species in captures per person-hour.

We performed paired t-tests between years (total captures per stand) for each data set. TCS samples were not significantly different between years: 1984 vs. 1985, $t = 1.16$, $P = 0.25$; 1984 vs. 1986, $t = 1.24$, $P = 0.22$; 1985 vs. 1986, $t = 1.85$, $P = 0.075$. PF samples were also not significantly different between years: 1984 vs. 1985, $t = 1.85$, $P = 0.072$. Consequently, we combined years for each sampling method for all analyses.

Statistical Comparisons

For each method, we tested for statistical differences in mean capture frequencies among age and moisture classes, across, within, and between inland and coastal areas. These tests were performed on the total herpetofauna, taxa at the level of class, order, and sub-order, and on those species captured on at least one third of our stands in either area.

Mean capture frequencies of each faunal grouping were tested for statistical differences among three forest age classes and three moisture classes. In cases where group variances were equal among classes, we used one-way analysis of variance (ANOVA). We used Hartley's F max test (Milliken and Johnson 1984:18) with $P \leq 0.01$ to determine the equality of variances for all three-group tests. We used $P \leq 0.01$ because

ANOVA is robust under moderate violations of the assumption of equal variances (Zar 1984:170). If a significant F-statistic resulted from the ANOVA test, we tested further for significant differences between pairs in order to isolate the source of the differences by using the Tukey test (TU) for multiple comparisons (Zar 1984:186). Where group variances were not equal or where one of the three age or moisture classes had no captures, we performed all pairwise tests (multiple comparisons) using the Games and Howell modification of the Tukey test (GHMC) (Keselman and Rogan 1978).

To test for statistical differences in capture frequencies in age and moisture classes between coastal and inland areas, we used two sample t-tests (Zar 1984:131). We followed the more conservative approach of not pooling variances. Between-area comparisons consisted of two families of tests: (1) a single paired comparison based on all stands, and (2) five pairwise comparisons defined by the different forest age and moisture classes. Tests in the first family were considered statistically significant at the $P \leq 0.05$ level. A Bonferroni adjustment (Miller 1981:67) was used for tests done within the second family to maintain an overall significance level of $P \leq 0.05$.

For the species richness analyses, stand records from the TCS and PF data were combined. The means of the total number of species for each forest age and moisture class were tested for differences described.

Also, the similarity of species' composition among equal numbers of stands (selected randomly) in each forest age class were determined by using Jaccard's similarity coefficient (Sneath and Sokal 1973:131):

$$S_j = \frac{a}{a + b + c}$$

in which, for any two classes, a = number of species in common, b = number of species in the first class

only, and c = number of species in the second class only.

RESULTS AND DISCUSSION

We sampled 25 species. Amphibians accounted for 97.8% (salamanders, 96.3%) of all captures, and reptiles 2.2%. The TCS method yielded more than 66% of all captures (table 2), sampling 22 species (table 3) and accounting for 67% of the amphibians and 85% of the reptiles. The PF method sampled 19 species (table 4) and accounted for slightly less than 1/3 of all captures (table 2).

Species Composition, Richness

Similarity Indices

Based on species presence-absence data, an analysis of faunal similarities between forest age classes

(coastal and inland areas combined) indicated that greatest similarity in species composition occurred between the mature and old-growth stands (table 5). Jaccard's Similarity Index (JSI) values, for comparisons between young and old-growth stands and young and mature stands, indicated that young stands were different in species composition from both classes of older forest stands. These differences were greatest between young and old-growth stands (table 5).

Species Richness

The number of species per stand for all 42 stands ranged from 3 to 13 (fig. 3). The coastal mature stands yielded the highest mean number of species overall, while the lowest mean number of species occurred on the inland mature stands (table 6, fig. 3). The

Table 2.—Captures of herpetofauna by time-constrained searches (TCS) and pitfall traps (PF) in Douglas-fir forests of northwestern California and southwestern Oregon from 1984 to 1986.

Method	Salamanders (mean ¹)	Frogs (mean)	Lizards (mean)	Snakes (mean)	All species (mean)	Total captures
PF 1984 ² (40 stands)	13.72 ±14.18	0.38 ±1.06	0.07 ±0.18	0.00 --	14.18 ±14.27	1021
PF 1985 ³ (40 stands)	11.20 ±10.23	0.32 ±0.83	0.21 ±0.61	0.02 ±0.15	11.76 ±10.19	508
PF Totals						1529 (32.6%) ⁵
TCS ⁴ 1984 (42 stands)	6.46 ±3.63	0.04 ±0.14	0.11 ±0.27	0.04 ±0.13	6.66 ±3.61	1118
TCS 1985 (42 stands)	5.80 ±3.80	0.01 ±0.20	0.15 ±0.30	0.06 ±0.16	6.11 ±3.81	1027
TCS 1986 (30 stands)	8.10 ±4.10	0.18 ±0.41	0.15 ±0.31	0.08 ±0.23	8.51 ±4.09	1021
TCS totals						3166 (67.4%)
Totals, both methods						4695

¹Mean for pitfall trapping = per 1000 trap-nights; X for time-constrained searches = per person-hour of search time; both are ± 1 standard deviation.

²PF 1984 = 50 trap-nights per stand.

³PF 1985 = 30 trap-nights per stand.

⁴All TCS = 4 person-hours per stand per year.

⁵Percentage of total captures.

Table 3.—Mean number of captures per person-hour¹ captured by time-constrained searches (TCS) in different age and moisture classes of Douglas-fir forests of northwestern California and southwestern Oregon in the springs of 1984, 1985, and 1986.²

Species	Young (11) ³	Mature (11)	Old-wet (6)	Old-mesic (10)	Old-dry (4)	Total old (20)	Total Captures
Frogs							
Tailed frog (<i>Ascaphus truei</i>)	0.000 —	0.008 ±0.025	0.000 —	0.013 ±0.040	0.000 —	0.006 ±0.028	2
Pacific treefrog (<i>Hyla regilla</i>)	0.049 ±0.128	0.166 ±0.263	0.028 ±0.068	0.117 ±0.153	0.000 —	0.067 ±0.123	44
Total	0.049 ±0.128	0.174 ±0.259	0.028 ±0.068	0.129 ±0.148	0.000	0.073 ±0.122	46
Salamanders							
Northwestern Salamander (<i>Ambystoma gracile</i>)	0.000 —	0.008 ±0.025	0.000 —	0.000 —	0.000 —	0.000 —	1
Clouded salamander (<i>Aneides ferreus</i>)	0.496 ±0.914	0.390 ±0.457	0.361 ±0.215	0.725 ±0.451	0.146 ±0.172	0.500 ±0.415	227
Black salamander (<i>A. flavipunctatus</i>)	0.099 ±0.178	0.121 ±0.272	0.000 —	0.050 ±0.070	0.000 —	0.025 ±0.055	35
Calif. slender ⁴ salamander (<i>Batrachoseps attenuatus</i>)	2.718 ±1.958	5.533 ±1.065	4.470 ±1.320	5.542 ±1.738	0.417 —	4.500 ±2.190	972
Pacific giant salamander (<i>Dicamptodon ensatus</i>)	0.091 ±0.183	0.008 ±0.026	0.000 —	0.008 ±0.026	0.021 ±0.042	0.008 ±0.026	12
Ensatina (<i>Ensatina eschscholtzii</i>)	2.265 ±1.653	2.595 ±1.391	2.625 ±2.321	4.508 ±2.816	2.938 ±1.332	3.629 ±2.506	1447
Del Norte ⁵ salamander (<i>Plethodon elongatus</i>)	0.278 ±0.411	0.396 ±0.970	1.722 ±2.237	2.278 ±3.349	0.208 ±0.191	1.622 ±2.607	258
Olympic salamander (<i>Rhyacotriton olympicus</i>)	0.000 —	0.038 ±0.086	0.070 ±0.111	0.192 ±0.258	0.000 —	0.116 ±0.203	31
Rough-skinned newt (<i>Taricha granulosa</i>)	0.038 ±0.101	0.140 ±0.183	0.028 ±0.068	0.192 ±0.399	0.021 ±0.042	0.108 ±0.290	49
Total	5.041 ±1.917	6.030 ±2.991	6.180 ±1.490	9.260 ±4.900	3.385 ±1.485	7.160 ±4.234	3032
Total amphibians	5.090 ±1.969	6.204 ±3.078	6.208 ±1.532	9.390 ±4.900	3.385 ±1.485	7.233 ±4.270	3078
Lizards							
Western skink (<i>Eumeces skiltonianus</i>)	0.008 ±0.025	0.045 ±0.101	0.000 —	0.008 ±0.026	0.063 ±0.125	0.017 ±0.058	10
Northern Alligator lizard (<i>Elgaria coeruleus</i>)	0.095 ±0.160	0.167 ±0.230	0.014 ±0.034	0.042 ±0.044	0.084 ±0.096	0.042 ±0.057	42
Southern Alligator lizard (<i>E. multicarinatus</i>)	0.000 —	0.008 ±0.025	0.000 —	0.000 —	0.063 ±0.125	0.013 ±0.056	3

(Continued)

Table 3.—(continued)

Species	Young (11) ³	Mature (11)	Old-wet (6)	Old-mesic (10)	Old-dry (4)	Total old (20)	Total Captures
Western fence lizard (<i>Sceloporus occidentalis</i>)	0.000 —	0.023 ±0.054	0.000 —	0.000 —	0.083 ±0.118	0.017 ±0.058	6
Total	0.102 ±0.170	0.242 ±0.313	0.014 ±0.034	0.058 ±0.068	0.292 ±0.323	0.092 ±0.173	61
Snakes							
Rubber boa (<i>Charina bottae</i>)	0.008 ±0.025	0.000 —	0.000 —	0.000 —	0.000 —	0.000 —	1
Sharp-tailed snake (<i>Contia tenuis</i>)	0.008 ±0.025	0.008 ±0.025	0.014 ±0.034	0.000 —	0.083 ±0.167	0.021 ±0.076	7
Ringneck snake (<i>Diadophis punctatus</i>)	0.000 —	0.057 ±0.109	0.000 —	0.008 ±0.026	0.073 ±0.086	0.019 ±0.048	11
Western aquatic garter snake (<i>Thamnophis couchii</i>)	0.000 —	0.008 ±0.025	0.000 —	0.000 —	0.000 —	0.000 —	1
Terrestrial garter snake (<i>T. elegans</i>)	0.015 ±0.050	0.000 —	0.000 —	0.000 —	0.000 —	0.000 —	2
Northwestern garter snake (<i>T. ordinoides</i>)	0.023 ±0.075	0.011 ±0.038	0.000 —	0.000 —	0.031 ±0.063	0.006 ±0.028	4
Common garter snake (<i>T. sirtalis</i>)	0.000 —	0.000 —	0.014 ±0.034	0.000 —	0.000 —	0.000 —	1
Total	0.053 ±0.086	0.083 ±0.138	0.028 ±0.043	0.008 ±0.026	0.187 ±0.239	0.050 ±0.122	27
Total reptiles	0.155 ±0.210	0.326 ±0.418	0.042 ±0.069	0.066 ±0.086	0.479 ±0.473	0.142 ±0.265	88
All herpetofauna	5.246 ±2.004	6.530 ±3.205	6.250 ±1.559	9.450 ±4.900	3.865 ±1.543	7.371 ±4.203	3166

¹Mean ± 1 standard deviation.²Data are from inland and coastal stands combined.³Number of stands.⁴Absent from inland stands.⁵Absent from coastal stands.

coastal stands had significantly more species per stand than the inland stands (fig. 3, table A1).

With coastal and inland areas combined, our mean species values indicated that species richness was greatest on mature stands (table 6), but was not statistically different.

In the inland area, the old-growth dry stands had the greatest mean number of species (table 6) but no comparisons yielded significant differences (fig. 3). Within the coastal

area, mean numbers of species were significantly different between forest age classes. Multiple comparisons (TU) indicated that the greatest differences occurred between young and mature stands (fig. 3).

The significantly higher number of species in the coastal vs. the inland area (fig. 3) is attributable to the salamander *Aneides lugubris* and four snakes (*Thamnophis couchii*, *T. sirtalis*, *T. elegans*, and *Charina bottae*), which were all sampled in very low num-

bers and only in the coastal area (tables 3-4). We believe this is an artifact of the difficulty of sampling for snakes in forested habitats (Bury and Corn 1987, Raphael and Marcot 1986, Welsh 1987). Most snake species exist in low densities, and available sampling methods only establish presence. All of these snake species occur in the inland area. The arboreal salamander, *Aneides lugubris*, is absent inland at the northern latitudes we sampled (Stebbins 1985).

Table 4.—Mean number of captures per 1000 trap-nights¹ captured by pitfall traps (PF) in different age and moisture classes of Douglas-fir forests of northwestern California and southwestern Oregon. Sampling occurred in the falls of 1984 and 1985.²

Species	Young (10) ³	Mature (11)	Old-wet (6)	Old-mesic (9)	Old-dry (4)	Total old (19)	Total Captures
Frogs							
Tailed frog (<i>Ascaphus truei</i>)	0.000 —	0.063 ±0.209	0.000 —	0.039 ±0.116	0.000 —	0.018 ±0.080	3
Western toad (<i>Bufo boreas</i>)	0.000 —	0.063 ±0.140	0.000 —	0.000 —	0.087 ±0.174	0.018 ±0.080	3
Pacific treefrog (<i>Hyla regilla</i>)	0.139 ±0.293	0.315 ±0.105	0.058 ±0.142	0.077 ±0.159	0.087 ±0.174	0.073 ±0.145	9
Yellow-legged frog (<i>Rana boylei</i>)	0.000 —	0.316 ±0.667	0.058 ±0.142	0.579 ±1.493	0.087 ±0.174	0.311 ±1.035	27
Total	0.139 ±0.293	0.473 ±0.948	0.116 ±0.179	0.694 ±1.483	0.260 ±0.332	0.420 ±1.039	42
Salamanders							
Northwestern salamander (<i>Ambystoma gracile</i>)	0.035 ±0.110	0.032 ±0.105	0.116 ±0.284	0.000 —	0.000 —	0.037 ±0.159	4
Clouded salamander (<i>Aneides ferreus</i>)	0.035 ±0.110	0.063 ±0.140	0.058 ±0.142	0.039 ±0.116	0.000 —	0.037 ±0.109	5
Black salamander (<i>A. flavipunctatus</i>)	0.035 ±0.110	0.410 ±1.250	0.000 —	0.193 ±0.352	0.087 ±0.174	0.110 ±0.260	20
Arboreal salamander (<i>A. lugubris</i>)	0.035 ±0.110	0.000 —	0.000 —	0.000 —	0.000 —	0.000 —	1
Calif. slender ⁴ salamander (<i>Batrachoseps attenuatus</i>)	0.298 ±0.422	2.153 ±1.162	0.463 ±0.401	2.517 ±1.037	0.347 —	1.476 ±1.322	72
Pacific giant salamander (<i>Dicamptodon ensatus</i>)	0.104 ±0.168	0.126 ±0.234	0.578 ±0.474	0.154 ±0.252	0.000 —	0.256 ±0.381	21
Ensatina (<i>Ensatina eschscholtzii</i>)	8.646 ±7.107	10.164 ±8.996	6.539 ±4.328	9.375 ±7.209	14.757 ±11.260	9.613 ±7.648	1097
Del Norte ⁵ salamander (<i>Plethodon elongatus</i>)	0.810 ±1.120	0.120 ±0.280	1.500 ±2.310	13.060 ±25.370	0.000 —	6.340 ±17.330	213
Olympic salamander (<i>Rhyacotriton olympicus</i>)	0.000 —	0.000 —	0.058 ±0.142	0.000 —	0.000 —	0.018 ±0.080	1
Rough-skinned newt (<i>Taricha granulosa</i>)	0.174 ±0.245	0.442 ±0.493	0.174 ±0.290	0.579 ±1.264	0.087 ±0.174	0.347 ±0.889	38
Total	9.620 ±7.340	12.280 ±8.590	8.510 ±4.680	18.750 ±21.040	15.020 ±11.380	14.730 ±15.710	1472
Total Amphibians	9.760 ±7.480	12.750 ±8.340	8.620 ±4.670	19.440 ±20.940	15.280 ±11.610	15.150 ±15.710	1514
Lizards							
Western skink (<i>Eumeces skiltonianus</i>)	0.000 —	0.095 ±0.225	0.058 ±0.142	0.000 —	0.087 ±0.174	0.037 ±0.109	5

(Continued)

Table 4.—(continued).

Species	Young (10) ³	Mature (11)	Old-wet (6)	Old-mesic (9)	Old-dry (4)	Total old (19)	Total Captures
Northern alligator lizard (<i>Elgaria coeruleus</i>)	0.035 ±0.110	0.000 —	0.000 —	0.039 ±0.116	0.260 ±0.521	0.073 ±0.248	5
Southern alligator lizard (<i>E. multicarinatus</i>)	0.000 —	0.000 —	0.000 —	0.039 0.116	0.000 —	0.018 ±0.080	1
Western fence lizard (<i>Sceloporus occidentalis</i>)	0.000 —	0.032 ±0.105	0.000 —	0.000 —	0.174 ±0.347	0.037 ±0.159	3
Total	0.037 ±0.110	0.126 ±0.321	0.058 ±0.142	0.077 ±0.153	0.521 ±0.601	0.164 ±0.335	14
Snakes							
Northwestern garter snake (<i>T. ordinoides</i>)	0.000 —	0.000 —	0.000 —	0.000 —	0.087 ±0.174	0.018 ±0.080	1
Total	0.000 —	0.000 —	0.000 —	0.000 —	0.087 ±0.174	0.018 ±0.080	1
Total reptiles	0.035 ±0.110	0.126 ±0.321	0.058 ±0.142	0.077 ±0.153	0.608 ±0.716	0.183 ±0.390	15
All herpetofauna	9.791 ±7.572	12.877 ±8.408	8.680 ±4.742	19.527 ±20.888	15.888 ±11.555	15.333 ±15.694	1529

¹Mean ± 1 standard deviation.²Data are from inland and coastal stands combined.³Number of stands.⁴Absent from inland stands.⁵Absent from coastal stands.

The fact that we generally found more species on older stands and that we found a greater similarity between mature and old-growth stands than between either of these older classes and young stands (see also Raphael, this volume) suggests that both the mature and old forest age classes provide more suitable habitat and a more diverse herpetofauna than young forests.

Relative Abundance Analysis

Differences Between TCS and PF

A notable aspect of our data is the differences between the TCS and PF methods—both in terms of kinds of

species and numbers of individuals captured. These differences follow from the different natures of these sampling methods. TCS is an active search method that permits the investigator to seek out animals where they hide. PF is a passive method that relies on animal surface movement or the seeking of shelter under trap covers (Welsh 1987.)

The results of our comparisons of salamander captures between coastal and inland areas using TCS and PF data, which appear contradictory, serve to illustrate the pronounced differences between the two methods. With TCS data, in all comparisons except the old-growth wet category, the coastal area had higher mean captures than the inland area.

This result was due to high captures (over 900 individuals) of a single species of salamander, *Batrachoseps attenuatus*, a species that occurred in all age and moisture classes. This species is absent inland. However, several factors unique to the inland area acted to counter the effects of the high captures of *B. attenuatus*. Those factors were the high captures of *Plethodon elongatus* (more than 250 captures), a species found almost exclusively on the inland stands, and higher relative captures of *Ensatina eschscholtzii* inland (865 inland vs. 580 coastal).

In contrast, results from PF, indicated significantly higher captures on inland stands than on coastal stands, for all stands combined (table A1).

PF captured few ($n=72$) of the highly sedentary *Batrachoseps attenuatus* relative to TCS ($n=972$). Captures of the relatively more vagile salamander species, *P. elongatus* and *E. eschscholtzii*, were greater on the inland stands than the coastal stands, for the PF data.

TCS provided a more complete data set, sampled more species (particularly reptiles) and had twice as many individuals as did PF (tables 2-4). The active nature of TCS accounts

for the disparities in capture numbers, and in the lack of consistency of statistically significant differences among forest age and moisture classes between these data sets, even for the same species (table A1). Most significant results from our analyses derived from the larger TCS data set. Subsequent discussion of results will refer to these data unless they are identified as PF data. Mean captures (\pm one standard deviation) for all taxa analyzed are found in tables 3

and 4. Results of all tests on both data sets, and test statistics for those tests with significant differences, are found in table A1.

Salamanders

Almost all captures (96.3%) were salamanders (table 2), consequently, the results of our analyses were essentially the same for all herpetofauna, amphibia, and salamanders (species combined) (table A1). Salamanders were not equally distributed among forest age classes. Testing the equality of mean captures among age classes, with coastal and inland areas combined, yielded significant differences. Multiple comparisons (TU) indicated these differences were between the young and old stands, with more captures on the old stands (fig. 4).

Salamanders were not equally distributed among forest moisture classes. Multiple comparisons (GHMC), with areas combined, indicated a significant difference in mean captures between the old-growth mesic and old-growth dry stands, with more captures in the mesic stands (fig. 4). These differences are probably a result of the fact that drier sites offer less equable habitat for amphibians. We also captured fewer

Table 5.—Jaccard similarity index (JSI) values for species of herpetofauna in 3 age classes of Douglas-fir forests of northwestern California and southwestern Oregon. Values were calculated using 10 randomly selected stands from each forest age class, including coastal and inland areas. Greater JSI values indicate greater similarity in species composition.

All stands (Areas combined)	Young	Mature	Old-growth
Mature	.542		
Old-growth	.467	.846	
Total number of species	16	21	15

Table 6.—Mean (\pm 1 standard deviation) numbers of species of herpetofauna among three age and three moisture classes of Douglas-fir forests of northwestern California and southwestern Oregon.

Inland stands	Young	Mature	Old-dry	Old-mesic	Old-wet
Number of stands	3	6	3	6	3
Mean number of species	5.67 ± 3.06	4.67 ± 1.51	6.67 ± 3.51	5.17 ± 1.33	6.33 ± 2.08
Total number of species	10	13	14	12	10
Coastal stands					
Number of stands	8	5	1	4	3
Mean number of species	5.50 ± 2.56	10.00 ± 2.92	6.00 —	9.25 ± 2.63	5.00 ± 2.00
Total number of species	16	21	6	15	10
All stands					
Number of stands	11	11	4	10	6
Mean number of species	5.55 ± 2.54	7.10 ± 3.51	6.50 ± 2.89	6.80 ± 2.78	5.67 ± 1.97
Total number of species	17	23	17	17	14

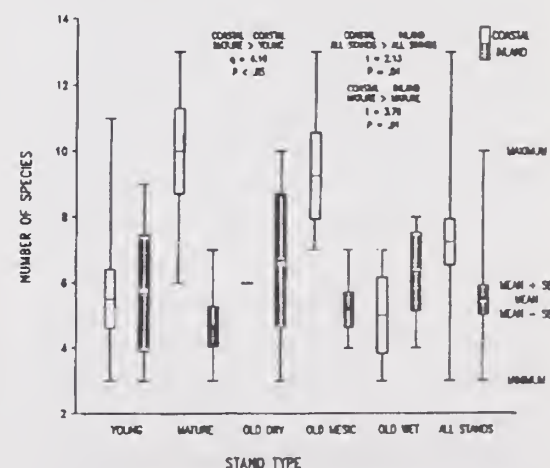


Figure 3.—Numbers of species of herpetofauna captured in the coastal and inland areas in three forest age and three forest moisture classes of Douglas-fir dominated forests from 1984-1986. Captures were by time-constrained search (TCS) and pitfall traps (PF).

amphibians on old-wet stands than old-mesic stands, although the difference is not statistically significant.

Within the coastal area, multiple comparisons (TU) indicated that both mature and old-growth mesic stands were significantly different from young stands, but not from each other, with the lowest mean captures occurring on the young stands (fig. 5a). Between-area comparisons for salamanders indicated a significant difference in means between coastal and inland mature stands (fig. 5a).

The PF data yielded no significant differences between mean captures in age or moisture classes with coastal and inland areas combined or within either area (table A1). However, comparisons between these areas indicated a significant difference with all stands combined (fig. 5b). The greatest differences occurred between the old-growth wet stands; however the results were not significant (fig. 5b).

The greater number of individuals in older stands parallel our findings of greater numbers of species in older forest age classes (table 6). As with the species richness analysis, the number of individuals was greater in older forests of the coastal area than in the inland area. These differences suggest that older forests support both a richer and more abundant salamander fauna.

The lower capture rates on old-wet stands compared to old-mesic was an unexpected result. We offer two possible explanations for these lower sample values. One possibility is that the habitat structure is more complex on these wet forest stands, with more and larger downed woody material, a thicker duff layer, and denser understory vegetation requiring more time to search and making it more difficult to find animals (TCS method) and making them less likely to be moving about on the surface and encountering our traps (PF method). A second possibility is that the wet stands actually contain fewer salamanders.

Salamanders play an important functional role in forest ecosystems because of several unique aspects of their ecology. Though they are small, with 90% of species having adult body masses less than those of small birds and mammals (Pough 1980), they are often a major portion of the vertebrate biomass in a forest. At the Hubbard Brook Experimental Forest in New Hampshire, a single species of salamander accounted for a greater portion of biomass and secondary productivity than any other vertebrate group (Burton and Likens 1975a,b). Their small size enables them to exploit prey too small to be used by birds and mammals and subsequently to convert these prey into biomass that is available to larger vertebrates (Pough 1983). Pough et al. (1987) cites both direct observations of predation and the ubiquity of defensive mechanisms among salamanders as evidence of their importance as a food source for both avian and mammalian predators. Because salamanders are ectotherms and have the lowest metabolic rates of any terrestrial vertebrates (Feder 1983), this biomass conversion process is extremely efficient, with 40-80% of the energy invested being used to produce new biomass (Pough et al. 1987). As a consequence of these characteristics, salamanders are quantitatively and qualitatively important components of food webs

of many forest ecosystems. The fact that their numbers appear to be reduced by certain forest practices could potentially affect energy flow and biomass production at all biological levels.

Frogs

Testing the equality of mean captures yielded significant differences in captures of frogs in coastal age and moisture classes, with significantly higher mean captures in old vs. young stands and mesic vs. wet stands (table A1). These results are attributable to a single species, the Pacific treefrog. No other significant differences were found (table A1).

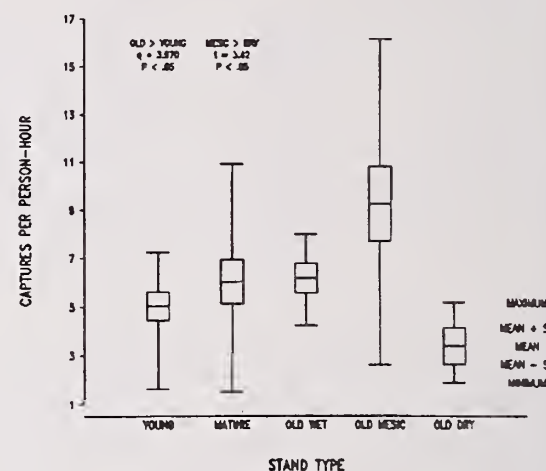


Figure 4.—Captures of salamanders per person-hour (TCS) in three forest age and three moisture classes. Data are from the coastal and inland areas combined, and sampling occurred from 1984-1986.

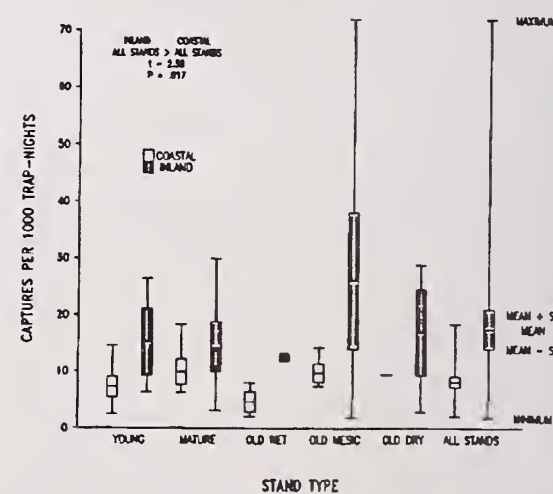
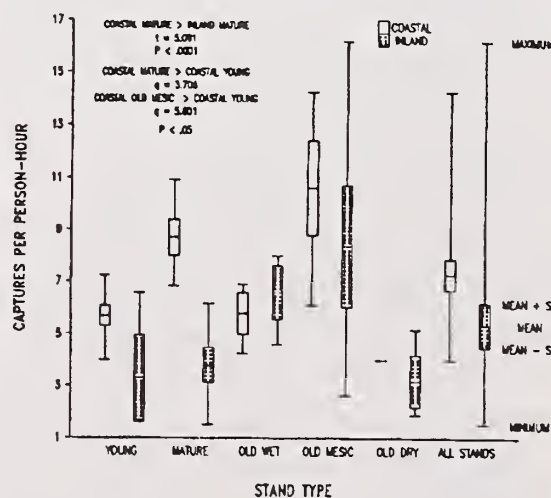


Figure 5.—Captures of salamanders per person-hour (A:TCS) and per 1000 trap-nights (B:PF) in the coastal and inland areas. Data are from 1984-1986 (TCS) and 1984-1985 (PF).

Reptiles

The reptile fauna in the forests of the Pacific Northwest is depauperate (Nussbaum et al. 1983, Stebbins 1985) with most species occurring in relatively low abundance (tables 3-4).

Distribution of reptile species, by age and moisture class, indicated about equal numbers of species in the young, mature, and old-growth age classes, with lower numbers of species in old-growth wet forests.

Based on TCS and PF data, our mean captures of reptiles (species combined) were higher on both drier and older stands, but the differences were not statistically significant. Our sample sizes were not sufficient to analyze for differences among age and moisture classes at the species level, except for the northern alligator lizard for which our data indicated no statistically significant association with a particular forest age or moisture class (table A1).

We did not sample in any recently harvested areas, but given their preferences for open areas and their related heliothermic natures, reptiles, particularly lizards, probably increase following logging, and through the early seral stages of regenerating forests (see Raphael, this volume). Raphael and Marcot (1986) indicated that the sagebrush lizard (*Sceloporus graciosus*) was four times

as abundant in early vs. late shrub stages.

Relative Abundance of Common Species

Common species (captured on at least one third of our stands in either area by either sampling method) were analyzed for differences in mean captures in age and moisture classes, across, within and between coastal and inland areas (table A1). Besides the northern alligator lizard, these species consisted of amphibians—2 frogs and 7 salamanders. Other amphibians whose distributions relative to forest age were considered noteworthy are also discussed.

Yellow-Legged Frog (*Rana boylei*).—This species was absent from all young stands (table 4), but they were also captured at such low frequencies on our inland stands as to preclude analyses within this area. Within the coastal area, no significant differences were found for capture frequencies of this species in forest age or moisture classes (table A1).

The yellow-legged frog is a highly aquatic species (Stebbins 1985) and therefore our PF captures (table 4) must be considered incidental. These captures may have been frogs seeking terrestrial overwintering cover above high water levels (PF sampling was done in the fall). However, this frog was absent from young stands. Three facts need be considered: (1) all but a single capture occurred in the coastal area; (2) in general, the coastal stands were closer to perennial streams and creeks than were the inland stands; (3) within the coastal area, only two out of eight young stands had PF grids near suitable aquatic habitat, whereas all the mature and old-growth stands had PF grids near such habitat. Thus we can not rule out the possibility that this frog's absence from young stands in our samples is an artifact of our stand locations relative to avail-

able and suitable aquatic habitat (Bury and Corn, this volume).

Twenty-one records from area-constrained aquatic surveys (H. Welsh, unpubl. data) were almost equally divided between creeks in young and mature forests. On the other hand, it is possible that older forests provide some particulars of microhabitat required by overwintering yellow-legged frogs not present in young forests.

Pacific Treefrog (*Hyla regilla*).—The Pacific treefrog is the only frog for which our data indicated significant differences in captures between both forest age and moisture classes (fig. 6). Within the coastal area, this frog was captured at significantly different frequencies in both forest age and moisture classes. However, these differences were not observed within the inland area, probably due to lower captures and higher variances on these stands (table A1).

Because the Pacific treefrog is not restricted to forested habitat (Stebbins 1985), we are suspicious of our data indicating greater abundance in older forests (fig. 6). Conceivably older forests provide more cover and foraging areas for this species than do young forests and thus support higher relative abundances. Most of our captures of treefrogs occurred in association with large downed woody material. However, we cannot rule out the possible influence of proximity of breeding sites on these results (Bury and Corn, this volume). The older forest stands were generally closer to standing water than the young stands (as with *Rana boylei*) in the coastal area.

The difference in captures of treefrogs between the mesic and wet moisture classes (fig. 6) may be an artifact of unequal detectability. Most treefrogs were captured by TCS and they are more easily exposed and seen by investigators in the more open understory of the mesic stands. The alternate possibility, that there are actually more treefrogs on mesic stands, is consistent with the in-

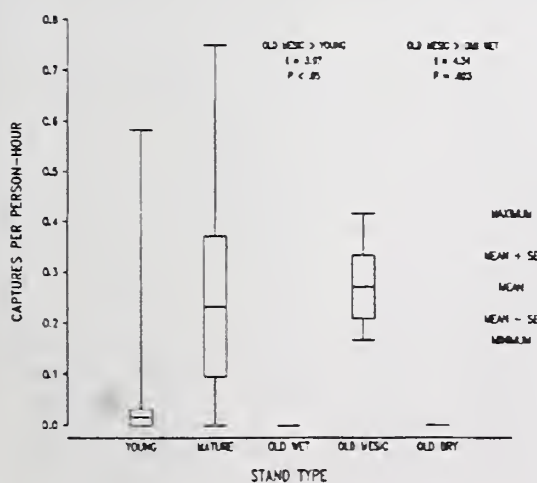


Figure 6.—Captures per person-hour (TCS) of the Pacific treefrog (*Hyla regilla*), in three forest age and three moisture classes. Data are from the coastal area from 1984-1986.

creased incident radiation in the mesic stands which would promote higher productivity of invertebrate prey, and thus possibly support more treefrogs.

The Tailed Frog (*Ascaphus truei*).—This frog was captured only on mature and old-growth stands (tables 2-3); however, the total number of captures (5) was too low for statistical tests. This species is of interest, nonetheless, because of its absence from young stands. The tailed frog, like the yellow-legged frog, is highly aquatic (Bury 1968, Stebbins 1985). Therefore these records based on terrestrial sampling are considered incidental. However, results from another study employing an area-constrained aquatic sampling method yielded more than 400 captures of tailed frogs (Welsh, in prep.). These data were consistent with the incidental records reported here; there were significant increases in tailed frog abundance with increased forest age.

Olympic Salamander (*Rhyacotriton olympicus*).—This species was absent from all young stands (tables 3-4). Low captures prompted us to combine moisture classes for the age analysis. Multiple comparisons (GHMC), coastal and inland areas combined, indicated that older stands had significantly greater numbers of Olympic salamander than young stands (fig. 7).

This species is restricted to headwater habitats, such as seeps, springs, and small creeks in forests where it prefers cold water flowing over rocky substrates (Anderson 1968, Nussbaum et al. 1983). Because of the relative scarcity of this microhabitat in the areas of our study, *Rhyacotriton* occurs in a patchy distribution. It can be abundant where conditions are suitable, but we found appropriate microhabitat islands for this species to be few, small, and widely scattered on our stands. This resulted in relatively few captures (tables 3-4). We found *Rhyacotriton* absent in younger forests (fig. 7),

which is consistent with results from other studies (Bury 1983; Bury and Corn 1988; Welsh, in prep.). This species appears to be sensitive to forest harvest practices because of its particular habitat requirements (Bury and Corn 1988; Welsh, in prep.). Current harvest practices do not protect headwater habitats. Such habitats are often radically altered by harvest practices, which can change water flow and temperature, increase sediment loads, and change the structure and composition of the riparian vegetation (Bury and Corn 1988). The result of these changes is often the extirpation of local populations of this species.

Clouded Salamander (*Aneides ferreus*).—Multiple comparisons (GHMC) indicated significant differences in mean captures of clouded salamanders between young and old stands in the inland area but not in the coastal area (fig. 8a). Testing for differences with coastal and inland areas combined revealed significant differences in mean captures among moisture classes; multiple comparisons (TU) indicated that the mesic stands had significantly higher mean captures than did dry stands (fig. 8b).

This species, a habitat specialist, occurs most often under exfoliating bark on downed conifer logs (Stebbins 1985, Nussbaum et al 1983). At several coastal redwood localities,

Bury (1983) and Bury and Martin (1973) found it to be more abundant in young stands than older stands. They attributed the differences to an increase in bark on downed woody material from logging. Our data from the coastal area (fig. 8a) indicated slightly more *A. ferreus* in younger than older forests, but the differences were not significant. However, in the inland area the clouded salamander was found in significantly higher numbers on old vs. young stands (fig. 8a). We suspect that these differences are due to the differences in moisture regimes between the two areas. This idea is supported by our findings of significant differences in capture means between mesic and

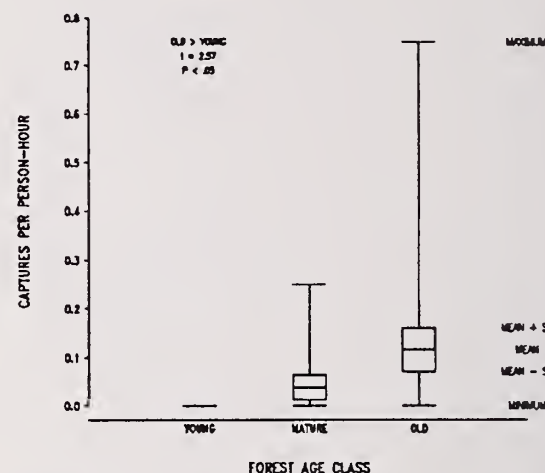


Figure 7.—Captures per person-hour (TCS) of the Olympic salamander (*Rhyacotriton olympicus*), in three forest age classes. Data are from the inland and coastal areas combined, from 1984-86.

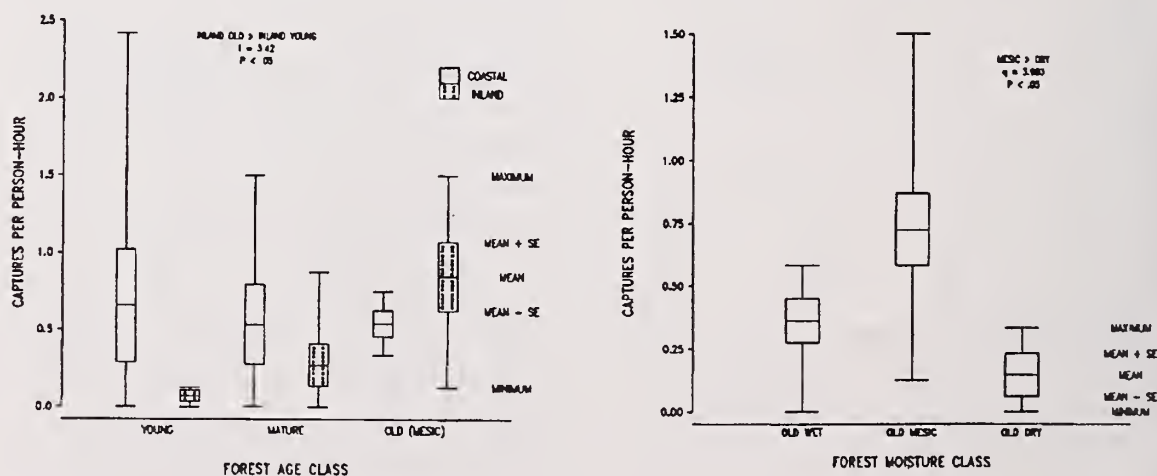


Figure 8.—(A) Captures per person-hour (TCS) of the clouded salamander (*Aneides ferreus*) in the coastal and inland areas, in three forest age classes. (B) Captures per person-hour (TCS) in three forest moisture classes; data are from coastal and inland areas combined. Sampling occurred from 1984-86.

dry old-growth sites (fig. 8b). We suggest that logs on inland young stands are subjected to higher evapotranspiration rates than are logs on old-growth stands because of greater incident radiation. Possible increases in clouded salamanders on young stands from an increase in slash and logs after harvesting may be outweighed by the loss of suitable microclimatic conditions due to increased exposure.

Black Salamander (*Aneides flavipunctatus*).—We found significantly greater numbers of this species in the coastal area than in the inland area (fig. 9). Lynch (1981) pointed out that inland populations occur in a patchy distribution charac-

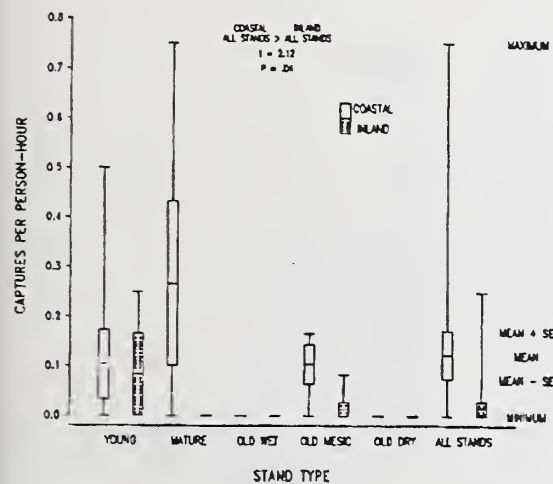
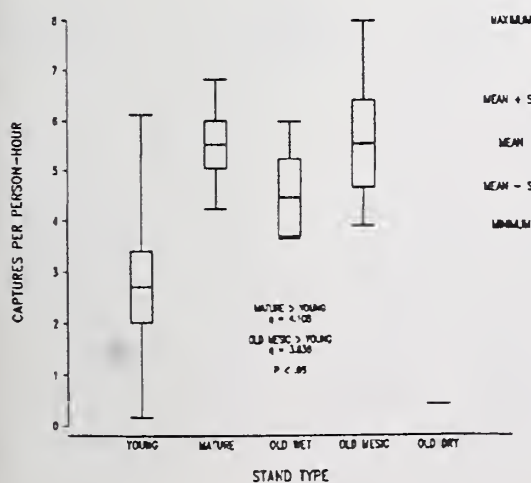


Figure 9.—Captures per person-hour (TCS) of the black salamander (*Aneides flavipunctatus*) in coastal and inland areas, in three forest age and three moisture classes. Data are from 1984-86.



teristic of a species on the decline. Further, he attributed the inland patchiness to climatic constraints and noted that the black salamander is restricted to low-lying suitable areas receiving at least 75 cm of annual precipitation. Its restriction to rocky habitats and its low relative abundance in northwestern California preclude drawing any conclusions from our forest age and moisture class analysis (table A1).

California Slender Salamander (*Batrachoseps attenuatus*).—The slender salamander, like the black salamander, appears to be restricted to low-lying suitable areas with relatively high annual precipitation (Maiorana 1976a). This species was absent from our inland sites, but accounted for the highest captures of any species within the coastal area. This was one of the few species we captured in sufficient numbers with both sampling methods to test both data sets for differences between forest age and moisture classes (see table A1). Within the coastal area, both TCS and PF data indicated significant differences in mean captures among forest age classes (figs. 10a-b). Multiple comparisons (TU) indicated that these differences were between both young and mature and young and old-growth stands (figs. 10a-b). Our findings here were consistent with trends found by others (Bury 1983, Bury and Martin 1973).

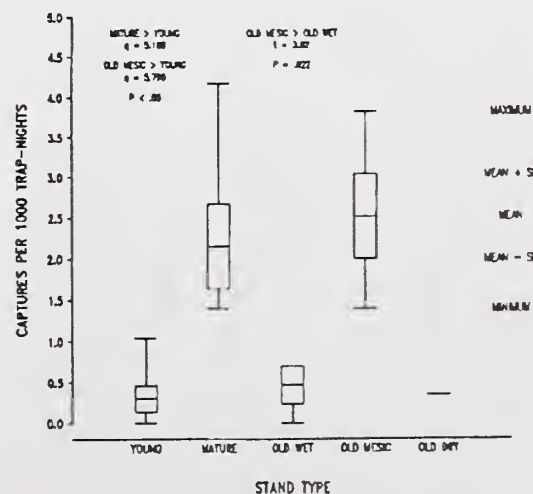


Figure 10.—Captures per person-hour (A:TCS), and captures per 1000 trap-nights (B:PF), of the California slender salamander (*Batrachoseps attenuatus*), in three forest age and three moisture classes. Data are from the coastal area from 1984-86 (TCS) and 1984-85 (PF).

The PF data showed a significant difference between captures in moisture classes, with a higher mean captures on mesic than on old-growth wet stands (fig. 10b), but the TCS data did not (fig. 10a). For a salamander species whose presence and relative abundance is correlated with relatively high and predictable moisture (Maiorana 1974, 1976a), this result is unexpected and may be an artifact of different sampling efficiencies between forest moisture classes. The old-growth wet stands appear to contain habitat with relatively great structural complexity: a thick and complex layer of understory, decomposing woody material, and mossy duff. Such habitat provides abundant microhabitat for a ground dwelling and semi-fossorial species like the slender salamander.

Slender salamanders may not frequent the surface as much to forage as they would on drier stands. Foraging in more protected areas would reduce exposure to predation and thus incur a selective advantage. Maiorana (1976b) termed this submergent behavior (our concept is a slight variation of her idea; she hypothesized that a species might actually forage less at times to avoid exposure to predation). As a result of less surface activity, fewer slender salamanders are captured in the pit-fall traps. The same logic can also be applied to the TCS method, in which lower captures would be expected in the structurally more complex habitat per unit of search time. With TCS, we did get slightly lower captures on old-growth wet stands for this species (table 3), but the active nature of TCS allowed us to detect enough slender salamanders that the capture rates between moisture classes were not significantly different.

Ensatina (*Ensatina eschscholtzii*).—Ensatina has broad ecological tolerances, occurring from relatively dry woodland habitats to moister forests at high elevations (Stebbins 1954). This species has the most extensive geographic distribu-

tion of all the western woodland salamanders, ranging from British Columbia to Baja California (Stebbins 1985). *Ensatina* were captured in the highest numbers of any species we sampled (table 3-4). There were significant differences in mean captures among forest age classes, with coastal and inland areas combined (fig. 11). Multiple comparisons (TU) indicated that old stands had significantly higher captures than young stands (fig. 11).

Both PF and TCS data indicated significant differences in mean capture frequencies between the coastal and inland areas (figs. 12a-b). Greater numbers were found on the inland stands. These differences between areas indicate that this species may be more abundant in the drier inland area than along the coast.

Del Norte Salamander (*Plethodon elongatus*).—Except for three captures from our most northern coastal stand, this species was sampled only on our inland stands. These salamanders are found primarily on or in rocky substrates (Stebbins 1985, Nussbaum et al. 1983), and reach high densities in talus and outcrops of fractured metamorphic rock. Such habitats were not present on some of our stands. Also, our study region encompassed the geographic range of this species, and all of our southern and some of our easternmost stands were beyond its geographic limits. Despite the patchy distribution of this species due to habitat restrictions, and absence from sites beyond its range, both methods indicated a higher relative abundance on older forest stands and a lower relative abundance on drier stands (figs. 13a-b, tables 3-4). These differences were not statistically significant; something we attribute to high variances within forest age classes resulting from this lack of appropriate microhabitat and the inclusion of stands beyond the range (table A1). A separate analysis of only stands from within the geographic range of the Del Norte salamander indicated that

the abundance of this species is significantly correlated with increased forest age (Welsh, in prep.).

Rough-Skinned Newt (*Taricha granulosa*).—Both TCS and PF showed a marked increase in captures of this species in older forests (figs. 14a-b, tables 3-4). Lack of statistically significant differences in captures between forest age classes (table A1) is probably related to specific habitat requirements of this species. We suspect that the critical habitat component was proximity to creeks or ponds, a breeding requirement for this species (Stebbins 1985). Many of our stands, particularly within the inland area, were a considerable distance from suitable breeding habitat for this newt. We had no TCS captures of this species on old-growth stands in our inland area, yet the rough-skinned newt is common there (Stebbins 1985, pers. observ.).

CONCLUSIONS

Our research indicates that salamanders comprise the majority of both species and individuals among the herpetofauna of the Douglas-fir/hardwood forests of northwestern California and southwestern Oregon. We found species diversity of the total herpetofauna to be greater in older forest age classes. Amphibians,

particularly salamanders, were significantly more abundant in older forests and significantly less abundant in drier forests.

We found the TCS method, actively searching for animals in their preferred microhabitats (usually associated with downed woody materials in these forest habitats), yielded more useful data on herpetofaunal diversity and abundance relative to forest age and moisture class than did PF. The TCS method sampled more individuals and species in addition to taking less time and expense than PF (see Welsh 1987).

Recent research in forested habitats (Bury and Corn 1988, Pough et al. 1987, Enge and Marion 1986, Bury

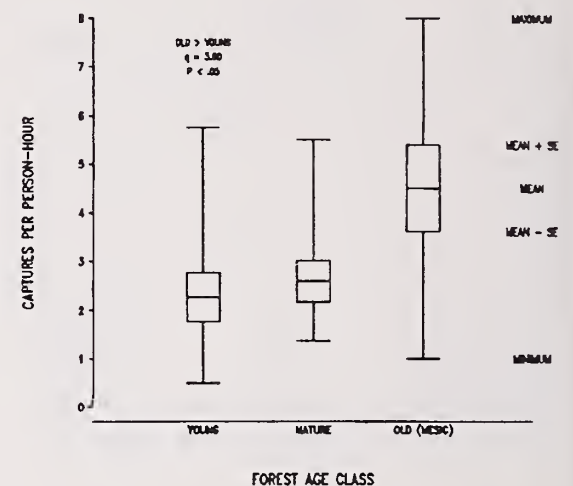


Figure 11.—Captures per person-hour (TCS) of *Ensatina eschscholtzii*, in three forest age classes. Data are from coastal and inland areas combined, from 1984-86.

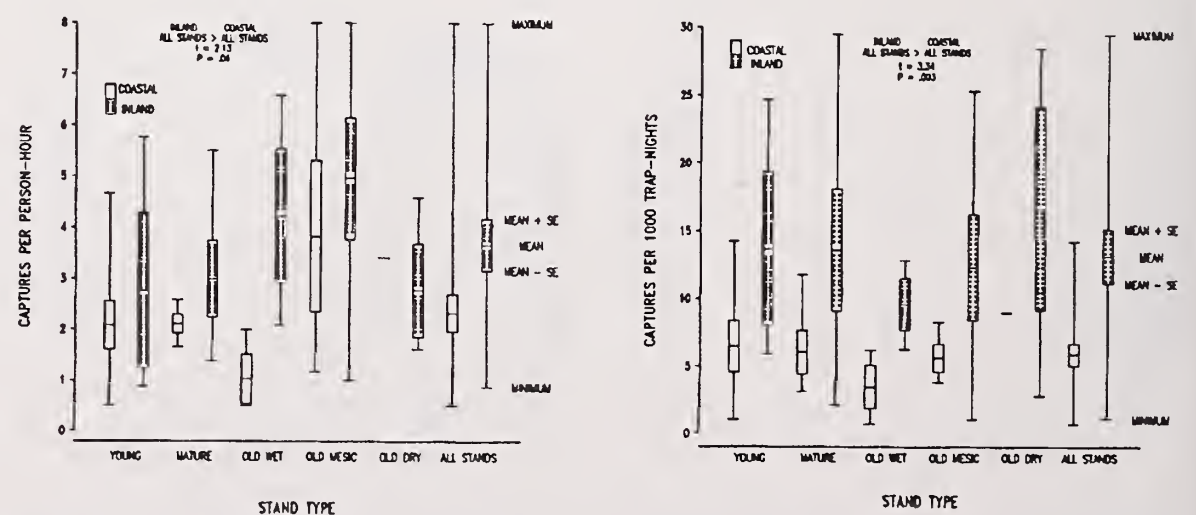


Figure 12.—Captures per person-hour (A:TCS), and captures per 1000 trap-nights (B:PF), of *Ensatina eschscholtzii* in coastal and inland areas, in three forest age and three moisture classes. Data are from 1984-86(TCS) and 1984-85 (PF).

1983, Bennett et al. 1980, Bury and Martin 1973) has indicated a pattern of fewer species and reduced abundance of herpetofauna after logging. We also found lower numbers of both species and individuals on younger stands.

Greater species diversity and greater relative abundance, for most species, on mature and old-growth stands may be related to greater structural complexity in older forests (Franklin and Spies 1984, Franklin et al. 1981). Older forests also have a narrower and more stable range of moisture and temperature than pre-canopy and young forests (Bury 1983, Harris 1984). Bury (1983) sampled amphibians on four paired

plots in coastal redwood forest, each pair consisting of a logged and an old-growth forest stand. He attributed the lower diversity and relative abundance of amphibians on the logged sites to microclimatic differences. Bury (1983) also found higher numbers of amphibians associated with a greater volume of downed woody material, but he considered these differences in cover habitat to be of secondary importance. Recently, Bury and Corn (this volume) found that coarse woody debris is related to salamander occurrence and abundance in the Oregon and Washington Cascades.

We believe that structural complexity or spatial heterogeneity (Pi-

anka 1966) plays an important role in promoting the addition of species and numbers of individuals in older forests. Downed woody material, besides affording cover, creates microclimatic pockets that can act to buffer the moisture and temperature fluctuations in the forest at large, and it provides protection from predation as well. Maiorana (1978) reported that space (small cavities and burrows) was more important in regulating relative abundance between two sympatric salamanders (*Aneides lugubris* and *Batrachoseps attenuatus*) than competition for food resources. Therefore, more salamander species and individuals should be expected in more structurally complex habitats. In fact, both microclimate and cover are probably interrelated, ultimate factors (Baker 1938) determining habitat suitability for temperate forest herpetofauna. Both are clearly affected by forest harvest practices and probably jointly account for most of the differences in diversity and abundance observed in the herpetofauna between young, mature, and old-growth forests in northwestern California and southwestern Oregon.

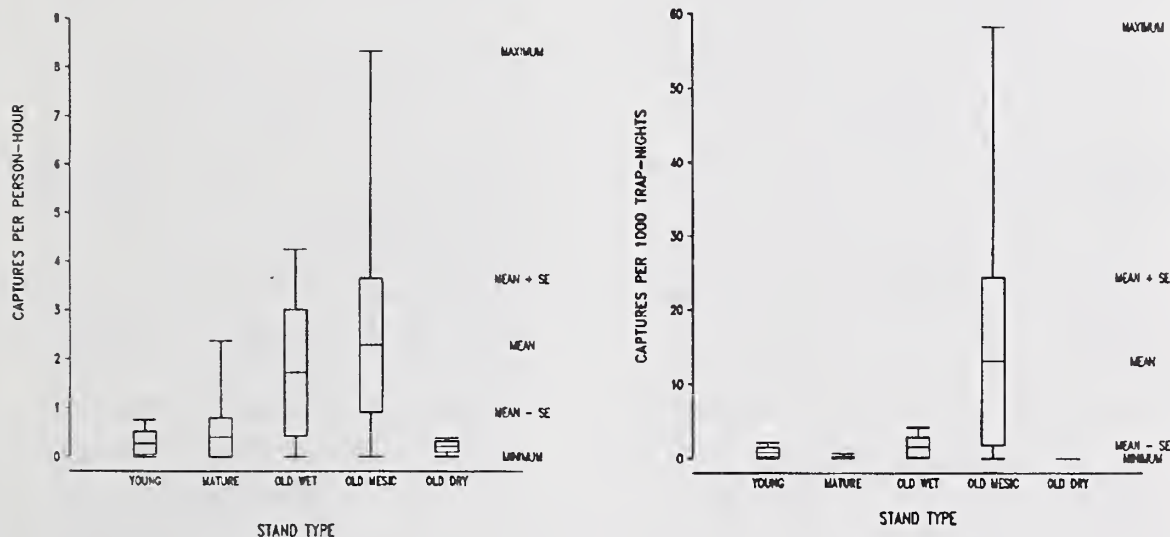


Figure 13.—Captures per person-hour (A:TCS), and captures per 1000 trap-nights (B:PF), of the Del Norte salamander (*Plethodon elongatus*), in three forest age and three moisture classes. Data are from the inland area, from 1984-86 (TCS) and 1984-85 (PF).

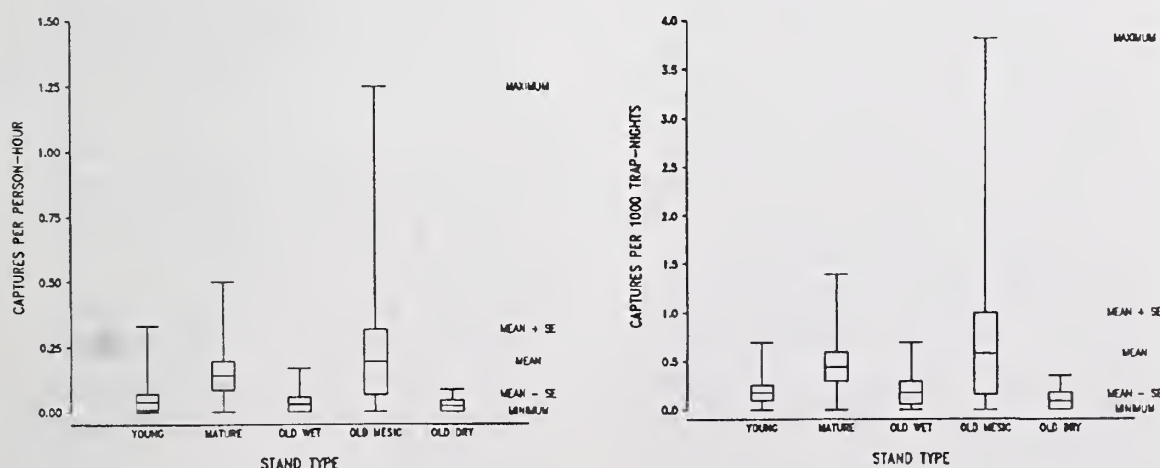


Figure 14.—Captures per person-hour (A:TCS), and captures per 1000 trap-nights (B:PF), of the rough-skinned newt (*Taricha granulosa*), in three forest age and three moisture classes. Data are from coastal and inland areas combined, from 1984-86 (TCS) and 1984-85 (PF).

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Table A1.—Comparisons of mean capture frequencies of herpetofauna, captured by two sampling methods time-constrained searches (TCS) and pitfall traps (PF), in three forest age and three forest moisture classes, and between coastal and inland areas.

	Inland stands		Coastal stands		Comparisons between coastal and inland stands						Stands combined	
	Moisture	Age	Moisture	Age	All stands	All old	Old wet	Old mesic	Mature	Young	Moisture	Age
Species richness												
TCS and PF data combined	*	*	*	F=5.20 .025>P>.01	C>I t=2.13 P=.04	+ ²	+	+	C>I t=3.70 P=.01	+	*	*
multiple comparisons:				mature>young q=4.160, P<.05								
All herpetofauna												
TCS data	*	*	F=10.75 .0025>P>.001	*	+	+	+	C>I	+	-	F=3.87 .05>P>.02	
multiple comparisons:				old>young q=6.035, P<.05 mature>young q=4.558, P<.05					t=5.51 P<.0001		mesic>dry t=3.22 P<.05	old>young q=3.860 P<.05
PF data	-	*	*	*	I>C t=2.44 P=.023	+	+	+	+	+	-	-
multiple comparisons:	*										*	*
Reptiles												
TCS data	-	*	*	*	*	+	+	+	+	+	-	-
multiple comparisons:	*										*	*
All lizards												
TCS data	-	*	*	*	*	+	+	+	+	+	-	-
multiple comparisons:	*										*	*
<i>Elgaria</i>												
<i>coeruleus</i>												
TCS data	-	*	*	-	*	+	+	+	+	+	*	-
multiple comparisons:	*			*							*	*
All snakes												
TCS data	-	*	*	*	*	+	+	+	+	+	-	-
multiple comparisons:	*										*	*
Amphibia												
TCS data	*	*	*	F=9.74 .005>P>.0025	*	+	+	+	C>I t=5.061 P<.0001	+	-	F=4.27 .025>P>.01
multiple comparisons:				old>young, q=5.091 mature>young, q=4.004 P<.05							mesic>dry t=3.49 P<.05	old>young q=3.998 P<.05
PF data	-	*	*	*	I>C t=2.43 P=.024	*	+	+	+	+	-	*
multiple comparisons:	*										*	*
All frogs												
TCS data	-	*	mesic>wet t=4.34 P=.023	-	*	+	+	+	+	+	-	-
multiple comparisons:	*			old>young t=3.97, P<.05							*	*
PF data	*	*	*	*	*	+	+	+	+	+	-	-
multiple comparisons:	*			*							*	*

(Continued)

Table A1.—(continued).

	Inland stands		Coastal stands		Comparisons between coastal and inland stands						Stands combined	
	Moisture	Age	Moisture	Age	All stands	All old	Old wet	Old mesic	Mature	Young	Moisture	Age
<i>Hyla regilla</i>												
TCS data	-	-	mesic>wet $t=4.34, P=.023$	-	*	+	+	+	+	+	-	*
multiple comparisons:	*	*		old>young $t=3.97, P<.05$							*	
<i>Rana boylei</i>												
PF data	3	3	*	-	*	+	+	+	+	5	3	3
multiple comparisons:				*							*	
All Salamanders												
TCS data	*	*	*	$F=8.67$ $.005>P>.0025$	*	+	+	+	C>I $t=5.091$ $P<.0001$	+	-	$F=4.26$ $.025>P>.01$
multiple comparisons:				old>young, $q=5.601$ mature>young, $q=3.706$ $P<.05$							mesic>dry $t=3.42$ $P<.05$	old>young $q=3.970$ $P<.05$
PF data	-	*	*	*	I>C $t=2.59$ $P=.017$	+	+	+	+	+	-	*
multiple comparisons:	*										*	
<i>Rhyacotriton olympicus</i>												
TCS data	-	-	*	-	*	+	+	+	+	6	-	
multiple comparisons:	*	*		*							*	old>young $t=2.57, P<.05$
<i>Aneides ferreus</i>												
TCS data	*	-	*	-	*	+	+	+	+	+	$F=4.45$ $.05>P>.025$	*
multiple comparisons:		old>young $t=3.42, P<.05$		*							mesic>dry $q=3.903, P<.05$	
<i>Aneides flavipunctatus</i>												
TCS data	3	-	*	*	C>I $t=2.12, P=.04$	+	3	+	+	+	3	-
multiple comparisons:		*									*	
PF data	-	-	*	-	*	+	3	+	+	+	-	-
multiple comparisons:	*	*		*							*	*
<i>Batrachoseps attenuatus</i>												
TCS data	4	4	*	$F=5.82$ $.05>P>.025$	4	4	4	4	4	4	4	4
multiple comparisons:				old>young, $q=3.836, P<.05$ mature>young, $q=4.108, P<.05$								
PF data	4	4	mesic>wet $t=3.62$ $.0025>P>.001$ $P=.022$	$F=10.94$	4	4	4	4	4	4	4	4
multiple comparisons:				old>young, $q=5.799, P<.05$ mature>young, $q=5.188, P<.05$								
<i>Ensatina eschscholtzii</i>												
TCS data	*	*	*	-	I>C $t=2.13, P=.04$	+	+	+	+	+	*	$F=3.72$ $.05>P>.025$
multiple comparisons:				*							*	old>young $q=3.60, P<.05$
PF data	*	*	*	*	I>C $t=3.34, P=.003$	+	+	+	+	+	*	*

(Continued)

Table A1.—(continued).

	Inland stands		Coastal stands		Comparisons between coastal and inland stands						Stands combined	
	Moisture	Age	Moisture	Age	All stands	All old	Old wet	Old mesic	Mature	Young	Moisture	Age
<i>Plethodon elongatus</i>												
TCS and PF	-	-	4	4	4	4	4	4	4	4	4	4
multiple												
comparisons:	*	*										
<i>Taricha granulosa</i>												
TCS data	3	-	*	-	*	+	+	+	+	+	-	-
multiple												
comparisons:		*		*							*	*
PF data	-	-	*	-	*	+	+	+	+	+	-	-
multiple												
comparisons:	*	*		*							*	

¹* = not significant at $P \leq .05$.

²+ = not significant at $P \leq .01$.

³Capture frequency in designated category was too low for analysis.

⁴Species absent from inland or coastal area.

⁵Absent from young stands.

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